The Red Alga *Chondrus crispus* Stackhouse (Irish moss) and Carrageenans—A Review

T. Chopin

Fisheries Research Branch
Gulf Region
Department of Fisheries and Oceans
Charlottetown, P.E.I.
C1A 4P3

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ABSTRACT

Chopin T. 1986. The red alga Chondrus crispus Stackhouse (Irish moss) and carrageenans - a review. Can. Tech. Rep. Fish. Aquat. Sci. 1514: v + 69 p.

The purpose of this review is to bring up-to-date knowledge on the red alga Chondrus crispus Stackhouse (Irish moss). This seaweed is a very commercially important marine plant along north Atlantic coasts from which polysaccharides, known as carrageenans, are extracted and used frequently in various industries (particularly in agro-foods, pharmaceuticals, and cosmetics) for their specific physical and chemical properties. The review deals on one hand with the biology, ecology, and physiology of the alga. On the other hand, it concerns the architectural organization, eco-physiological role, seasonal variations, and utilization of carrageenans.

RESUME

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Cette revue a pour but de mettre à jour les connaissances acquises sur l'algue rouge Chondrus crispus Stackhouse (mousse d'Irlande). Cette espèce est commercialement très importante le long des côtes de l'Océan Atlantique Nord en raison des polysaccharides qui en sont extraits: les carraghénanes. Ces derniers sont abondamment utilisés dans différentes industries (notamment en agro-alimentaire, pharmacie et cosmétique) pour leurs propriétés physico-chimiques particulières. La revue traite d'une part de la biologie, de l'écologie et de la physiologie de l'algue, et d'autre part, de l'organisation architecturale, du rôle éco-physiologique, des variations saisonnières et de l'utilisation des carraghénanes.

INTRODUCTION

The red alga Chondrus crispus Stackhouse is common along the coasts of the north Atlantic Ocean and has been used for more than a thousand years in human food (Thorbjarnason 1939).

Although it is one of the more frequently studied macroalgae during the last five decades, it is surprising to note that many aspects of its biology, eco-physiology, and biochemistry are still not well known. As a matter of fact, this seaweed has always aroused the curiosity of workers, for two reasons especially: its polymorphism and the large amount of sulphurylated polysaccharides, known as carrageenans, it produces.

The two most recent reviews are now 18 and 13 yr old (see MacFarlane 1968; Harvey and McLachlan 1973). The first dealt with biology and harvesting activities; the second was a collaborative work on aspects of biology, cytology, physiology, and biochemistry.

It would now seem useful to update our knowledge as much has been accomplished in both biology and the biochemistry of carrageenans (from "carragheen," a word of gaelic origin; a little village, near Waterford in Ireland, bears this name).

I. CHONDRUS CRISPUS STACKHOUSE

A. NOMENCLATURE

The first denomination seems to have been Fucus filiformis (Hudson 1762), although it was never approved and became Fucus crispus (Hudson 1778). Stackhouse (1797), recognizing the necessity to separate some taxons from the genus Fucus Linne, then proposed Chondrus crispus which is the only appellation to be used (Papenfuss 1950). However, the terminology is still undecided since Stackhouse (1809), in order to take into account the synonymy Fucus polymorphus Lamouroux (1805), created the genus Polymorpha. Lamouroux (1813) accepted in turn the generic name Chondrus and created the species Chondrus polymorpha.

Vernacular names are numerous in the countries where there was early use of this seaweed. They are derived from this use or the morphology. For example:

- in French: carraghen, goémon blanc, goémon frisé, goémon rouge, lichen, lichen blanc, lichen - carraghen, lichen rouge, mousse d'Irlande, mousse perlée, petit goémon;

- in Breton (Le Berre 1964): bejin bihan, bejin gwenn, bouch, bouchonou, bouch farda youd (Poulgoazec), bouch gad, bouch gwenn (Portsall), jargod (Perros), karraghen, liken (North Finistère), liken karraghen, ougnachou-ru (Poulgoazec), pioka (North Finistère), teles, tilez (Porspoder);

- in English: carrageen, carrageen moss, curly moss, curly gristle moss, Dorset weed, gristle moss, Irish moss, jelly moss, lichen, moss, pearl moss, pearly gristle moss, rock moss, sea moss, sea pearl moss, white wrack;

- in Gaelic: cairgin, carragheen, killeen, mathair an duilisg;

- in Icelandic: fjǿrugrǿs;

- in Norwegian: carragheen-tang, driesflik, gelatintang, krusflik;

- in Spanish: carragen, liquen, liquen de Irlanda, liquen de mar, musgo de Irlanda, musgo perlado;

- in Portuguese: botelho crespo, folha, folhinha, musgo da Irlanda;

- in Japanese (Mikami 1965): hirakotoji, tochaka, tsunomata.

B. TAXONOMY

The distinction of Chondrus from the genus Fucus done by Stackhouse in 1797 has been accepted by numerous authors (Lamouroux 1813; Lyngbye 1819; Greville 1830; Hooker 1833). C. crispus has been recognized as a member of Floridées by Lamouroux (1813) and of Florideae by C.A. Agardh (1817, under the name Sphaerococcus crispus) and since has always been considered as a red alga whatever the name that has been given to this group:

- Division: Rhodophyta (Wettstein 1901)

- Class: Rhodophyceae (Ruprecht, 1851)

- Sub-class: Florideophycidae (Lamouroux 1813)
  Florideophyceae (Cronquist 1960)

particularly because of its rhodoplasts, pit connections, non-flagellated spermatia, and carpogonial branch.

C. crispus belongs to the order of Gigartinales, defined by Schmitz (1892), whose main characteristics are the lack of gonophorus and the appearance of one auxiliary cell formed before fecundation and made of one intercalary cell of a lateral carpogonial branch. In this order, composed of 21 families, C. crispus belongs to Gigartinaceae in which Kylin (1956) recognized five genera: Mastocarpus (Gigartina), Chondrus, Iridaea, Rhodoglossum, and Besa. Since, Besa has been transferred from the Gigartinaceae to the Phyllophoraceae (Mikami 1965; Abbott and Hollenberg 1976). Gonimoblasts are diffuse among the filamentous cells of the medulla at the tips of the female gametophyte fronds, and carposporangia are mixed with vegetative tissues. Tetrasporophytes produce masses of cruciated tetrasporangia from medullary filaments also at the tips of fronds.

The number of species of Chondrus is uncertain. C. crispus is the only one recognized for the north Atlantic Ocean. Mikami (1965) listed seven species in Japan, among them C. ocellatus Holmes forma crispus Okamura would be a synonymy of C. crispus Stackhouse. Taylor (1945) reported the possible occurrence of two species of Chondrus in the Galapagos Islands: C. hancockii and C. albemarlensis. Taxonomy and nomenclature of forms of C. crispus remain confused; we will refer to this subject in the paragraph concerning the polymorphism of this species.

C. ANATOMY

The anatomy of the erect frond of C. crispus was described for the first time by Kützing (1843). It has an organization of the multiaxial cladomial type (Kylin 1917; Fritsch 1945).

The central medullary area is composed of large cells (14 to 40 µm in diameter, as much as three times more length than breadth) elongated along the longitudinal axis of the frond. They are colourless, and each has a reticulated parietal leucoplast (Darbishire 1902) and several nuclei (Grubb 1925). Primary and secondary pit connections bind the cells (Darbishire 1902; Tunmann 1909; Kylin 1917; Rosenvinge 1931; Fritsch 1945).

From the medullary area radiate, at intervals, filaments which constitute the inner cortex: three to five rows of smaller cells (7 to 10 µm in diameter) with an irregular shape, rich in floridean starch granules, and frequently having prominent secondary pit connections (Taylor and Chen 1973).

Resulting from the branching out of the inner cortex, the external cortex is formed generally of six rows of joining cells considerably decreased in size (3 to 4 µm in diameter), each one possessing a discoid rhodoplast. This is the assimilatory tissue.

A thick, colourless cuticular envelope covers the surface of the thallus (Fritsch 1945). During active growth, it may peel off (Prince 1971; Chen and McLachlan 1972). It is probably this cuticule that gives to some thalli of C. crispus (especially those living in shaded places or tide pools) their opalescent reflection in apical parts. According to Hanic and Craigie (1969), the cuticle is of proteinic nature.

Hyaline hairs appear on the surface of fronds (Rosenvinge 1931; Prince 1971). Their swollen base lies among external cortex cells, and extensions protrude through the cuticle.

The holdfast, adhering closely to the substratum and conforming to its contours, thickens from margin to center. It is composed of vertical rows of almost square cells (Darbishire 1902). The apical ones give rise to upright shoots which develop into branched fronds. The holdfast is also covered by the cuticle.

D. POLYMORPHISM

To describe a typical morphology for C. crispus is difficult because this species can have so many different shapes. We will give some general characteristics before approaching the problem of polymorphism.

From the holdfast, one or many erected fronds grow. Several fixation discs can be also placed side by side, resulting in spore coalescence (Ring 1970; Taylor and Chen 1973; Tveter and Mathieson 1976; Tveter-Gallagher and Mathieson 1980). The result is that C. crispus often looks like a clump with a crustose base covering the substratum. Plants vary by size, number of ramifications, dichotomy plane, width, thickness, and consistency. Thus, one can observe specimens small or large, with few or many branches, in the same or many planes, subcylindrical or with broad expansions, thick and cartilaginous or very flat and membranous, with truncated or bifid tips. The colour is changeable according to location and season: from dark purple-red, to yellow-greenish, through violet-brown.

The polymorphism of C. crispus was recognized early on as attested by the denominations Fucus polymorphus Lamouroux (1805) and Polymorpha Stackhouse (1809). Unfortunately, the polymorphism question is yet unresolved.

The number of recognized varieties varies according to the authors:

- in 1802, Turner described nine varieties;
- in 1808, Turner described ten varieties;
- in 1813, Lamouroux described 35 varieties;
- in 1819, Turner described ten varieties;
- in 1819, Lyngbye described seven varieties;
- in 1846-1851, Harvey described two varieties;
- in 1902, Batters described nine varieties;
- in 1931, Rosenvinge described ten varieties;
- in 1931, Newton described nine varieties;
- in 1947, Levring described four varieties;
- in 1938, Thomas described 22 varieties;
- in 1957, Newton et al. described six varieties;

and the synonymy is confused (Table 1).

Chopin (1985), using the Harvey (1846-1851) definition, considered two of the most contrasting forms of C. crispus in order to avoid possible discrepancies resulting from the variety determination (Fig. 1):

Table 1. Variety and form synonymy of Chondrus crispus Stackhouse cited by Turner (1802), Lyngbye (1819), Rosenvinge (1931), and Thomas (1938) [from Taylor and Chen (1973)].

Turner (1802)	Lyngbye (1819)	Rosenvinge (1931)	Thomas (1938)
Fucus crispus	Chondrus crispus	f. typica	f. typica
		abbreviata Kjellm. in Kylin	abbreviata Kjellm. in Kylin
		aegagropila Rosenv.	aegagropila Rosenv.
δ aequalis	γ aequalis	aequalis Lyngb.	aequalis (Good. and Woodw.) Kylin
			angustifrons Le Jol.
		ciliatus Suhr	ciliata Suhr ex Rosenv.
			corymbosa (Ag.) M. Thomas
		densa Rosenv.	densa Rosenv.
			dilatata M. Thomas
ε filiformis	δ filiformis		filiformis (Huds.) M. Thomas
			genuina Kütz.
	ζ incurvatus	incurvata Lyngb.	incurvata (Lyngb.) M. Thomas
η lacerus			lacera (Stackh.) M. Thomas
		membranacea Rosenv.	membranacea Rosenv.
			nana M. Thomas
ζ patens			
φ planus			plana (Turn.) Kütz.
			polychotoma Kjellm. in Kylin
			prolifera Kjellm. ex M. Thomas
	ε pumilus		
φ sarniensis			
γ stellatus	stellatus	stellata (Stackh.) Lyngb.	stellata (Good and Woodw.) Stackh.
	η uncinatus	uncinata Lyngb.	uncinata (Lyngb.) M. Thomas
			undulata M. Thomas
β virens			

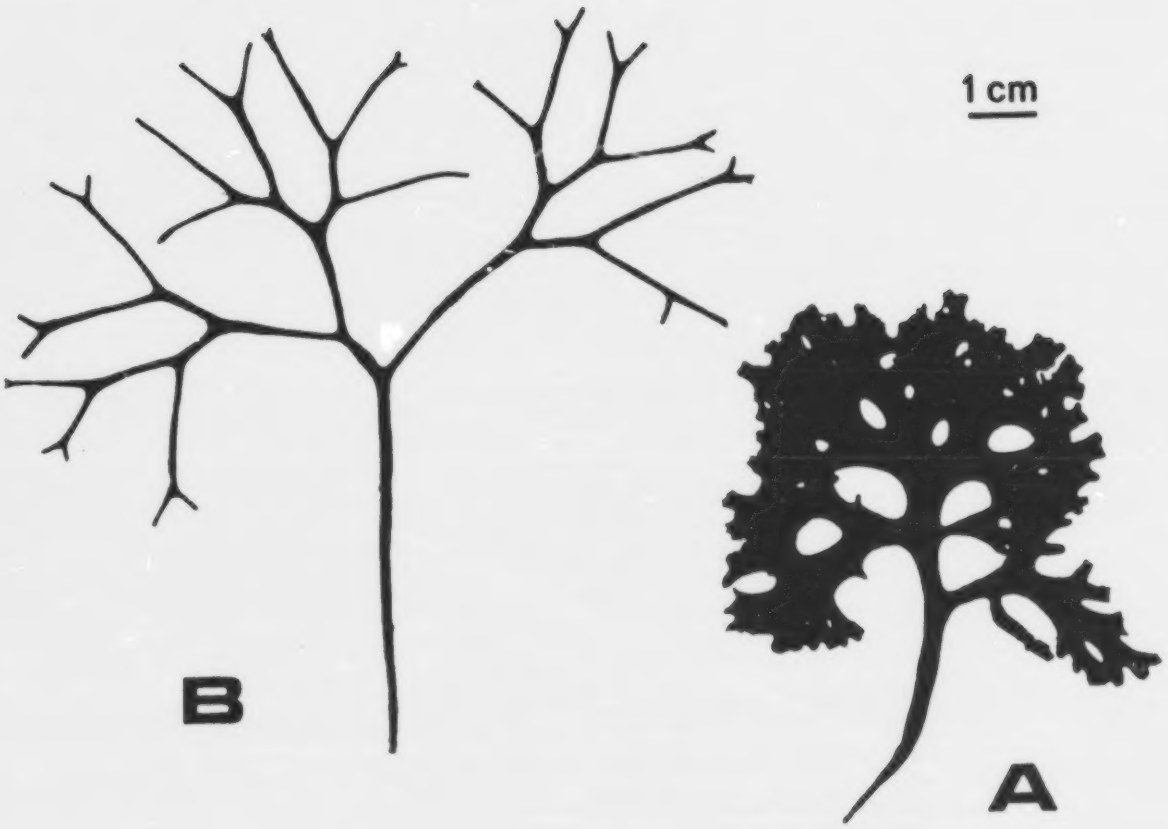

Figure 1. Two contrasting forms of Chondrus crispus studied by Chopin (1985):

- mediolittoral form (A);
- infralittoral form (B).

- a large form, thin and membranous, with round tips and maximum population density at a high level among Ascophyllum nodosum. Relative to its localization on the shore, Chopin (1985) called it "mediolittoral," according to Feldmann (1957) terminology. Following Newton et al. (1957), it would be the variety typica Turner;

- a narrow form, subcylindrical and cartilaginous, with sharp tips and maximum population density at very low tide among Laminariales. Chopin (1985) called it "infralittoral," and it would be the variety aequalis Turner.

Certain authors deemed morphological variation attributable to different ecological parameters (Darbishire 1902; Haas and Hill 1921; Thomas 1938). For example, size and width variability was due to wave exposure and currents (Newton 1931; MacFarlane 1964; Lilly 1968), salinity (Rosenvinge 1931; MacFarlane 1968; Mathieson and Burns 1975), or depth (MacFarlane 1966; Edelstein et al. 1969; Prince 1971; Mathieson and Burns 1975). Colour was dependent on light intensity (Kylin 1907; MacFarlane 1956), or quantity of available nutrients, especially nitrogen (Neish and Fox 1971). Thomas (1938) suggested polymorphism was a multifactorial phenomenon involving salinity, light, immersion duration, temperature, water motion, silting, and animal grazing.

Newton et al. (1957) felt environmental factors influenced the morphology of C. crispus as well. They considered that some of the so-called varieties were different stages of the development of the same plant, and they came to the conclusion that none of these forms are really varieties. MacFarlane (1968) used the term "ecological types."

However, the transition between infralittoral forms and those located in the upper part of the mediolittoral level is not clearly established. Between these extreme forms a whole series of intermediate forms exist (with a kinship not precisely defined) and which, in addition, can be observed within a few centimeters in the same population. Consequently, it appears that environment alone cannot explain entirely the morphological heterogeneity. The influence of genetics and environment can be determined only by an experimental approach (Hanic and Pringle 1978).

To this end, some authors carried out different kinds of experiments. Floc'h (1969) transplanted two of the most contrasting forms [in the Harvey (1846-1851) definition] to their reciprocal habitats: the large form from high-tide level and the narrow form from low-tide level (4 m difference). After 7 mo, growth of young specimens and adult ones which had been sectioned beyond their first dichotomy was observed: change of level (and therefore of ecological factors) had no determinant influence on morphology, as no alteration of the shape of each transplanted individual was noticed. Floc'h concluded that if these forms are not stable, adaptation to environment can only then be slow (and, in any case, beyond 7 mo); if, on the other hand, forms are permanent and transmitted to the next generation, one has to admit that they are at least different varieties. The shortness of the study and the fact that it was conducted on plants that had already well canalized morphogenetic potentialities compel us to be prudent in any conclusion.

Chen and Taylor (1978) cultivated in vitro, in seawater medium with growth regulators, explants (2 mm cubes) of medullary tissue from female gametophytic fronds with narrow and thick ramifications. After 5 mo, growing thalli present morphological characteristics of the plant from which they originated.

Guiry (1979) showed differences in duration of formation of reproductive organs (tetraspores and carpospores) in two forms of C. crispus (one broad and thin from Scotland, the other narrow and thick from the south of England) when cultivated in the same conditions of temperature, light intensity, and photoperiod. Although recognizing the necessity of more elaborate studies, he suggested that there are several morphologically distinguishable entities under the determination C. crispus.

Hanic (1973) conducted caryological research on C. crispus from Prince Edward Island and Nova Scotia, Canada. The number of chromosomes he found was n = 32 to 35 in gametophytes. As Magne (1964) found n = 30 for those from Brittany coasts in France, Hanic suggested that European and North American taxa might be different species. He cautioned, however, that the chromosomes are small and difficult to distinguish. He debated the value of the Atlantic Ocean as a barrier for speciation. He emphasized that if the chromosome number were the same on both sides of the Atlantic Ocean, it would not necessarily mean that they are conspecific, because number itself may not be a species criterion. Hanic suggested three-dimensional, ultrastructure studies of chromosomes and hybridizations from stable, morphological strains to elucidate this problem.

Published work on the first is not available; however, the second ones have been attempted. Chen and Taylor (1980a and b), after showing structural and anatomical differences between two contrasting forms of C. crispus (one broad and thin-growing in the Bay of Fundy, the other narrow and thick at the southeastern portion of the Gulf of St. Lawrence), cultivated them together in two series of environmental conditions over 10 mo. No convergence of form was observed. In addition, each form changed with different morphogenetic responses when subjected to different conditions of aeration, temperature, illumination, and photoperiod. As well, hybridization attempts over 13 mo failed while simultaneous fertilization between intrastrain males and females took place. These authors concluded that there is a strong, genetic differentiation between the two populations. However, one has to notice that the shortness of the experimental study and choice of the parental stock should be criticized here too.

E. GEOGRAPHICAL DISTRIBUTION

C. crispus is the only recognized species of the genus in the north Atlantic Ocean flora (Fig. 2). Along European coasts, one can observe this alga from Norway's North Cape to Morocco (71°N to 34°N), while along American coasts it can be observed from northern Newfoundland to Cape Hatteras (52°N to 35°N) (Taylor 1957; Wilce 1959; van den Hoek and Donze 1967; MacFarlane 1968; R.G. Hooper,[1] pers. comm.). The most dense populations occur in the

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[1]R.G. Hooper, Department of Biology, Memorial University of Newfoundland, St. John's, Nfld. A1B 3X9, Canada

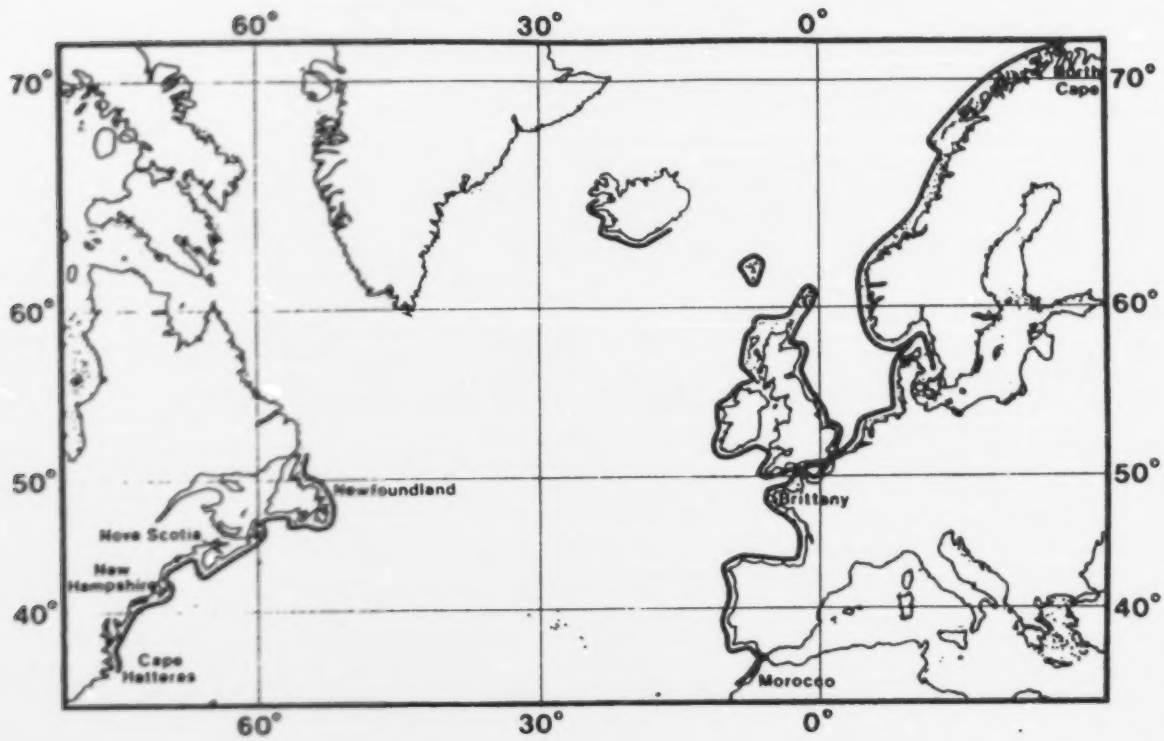

Figure 2. Geographical distribution of Chondrus crispus.

middle of each distribution: Ireland/England/France and New England/Maritime Provinces of Canada.

If one considers that distribution of marine algae is largely correlated to seasonal and latitudinal differences in temperature (Setchell 1893; 1917; 1935; Hutchins 1947; Gessner 1970; van den Hoek 1982), it appears that C. crispus is eurythermal. As a matter of fact, according to Taniguti (1962) and Michanek (1979a), it spreads out from subarctic to warm temperature climatic regions.

F. VERTICAL ZONATION

C. crispus grows from mid-tide level to 10-20 m below mean low tide (Rosenvinge 1931; MacFarlane 1952; 1956; Lamb and Zimmerman 1964; Floc'h 1967; MacAllister et al. 1967; Norton et al. 1969; Prince 1971; Mathieson and Burns 1975; Pringle and Semple 1980). However, Davis (1911) dredged it from 38 m; and, on exposed shores, it occupies the upper mediolittoral level where it spreads out in rocky crevices and tide pools (Darbishire 1902; Lilly 1968; MacFarlane 1968).

Highest densities (3 to 5 $kg \cdot m^{-2}$) occur from mean low-tide level (Darbishire 1902; MacFarlane 1952; Fott 1959; Colinvaux 1966; Pringle and Semple 1980) to 6 m below (Lamb and Zimmermann 1964; MacFarlane 1966; 1968; Prince 1971; Mann 1972; Mathieson and Burns 1975).

G. FACTORS CONTROLLING DISTRIBUTION AND ABUNDANCE

Availability of solid substratum is the major factor determining the distribution and the abundance of C. crispus. Most extensive populations are found on rocky shelves. Colonization of boulders and pebbles is more common on protected than on exposed shores where populations are reduced in density by scouring. Gibb (1938), Marshall et al. (1949), and Floc'h (1967) report C. crispus on infralittoral sandy bottom. This species is able to grow on encrusting Corallinaceae (MacFarlane 1968) but is rarely epiphytic on non-encrusting algae. Rosenvinge (1931) observed it once only on a Laminaria hyperborea stipe. It can be also noticed occasionally on the shells of bivalves and gastropods.

Substrate topography likewise influences abundance (Mathieson and Burns 1975). Most dense populations are observed on horizontal or slightly sloped surfaces. Vertical walls, which dry up more rapidly and are more exposed to waves (Lewis 1964), are often colonized by Mastocarpus stellatus; intermediate habitats are covered with mixed populations.

C. crispus grows abundantly on semi-exposed shores and in estuaries where currents are strong (Hehre and Mathieson 1970). On the other hand, abundance is reduced on exposed shores (MacFarlane 1966, 1968; Lilly 1968; Munda 1972). Conover (1968) found that productivity in situ is maximum at 2.3 knots and suggested that diffusion and transport of dissolved substances are proportional to current velocity. Consequently, algal metabolism is enhanced in agitated and turbulent waters. Water motion may also have an

important role in the dispersal of extracellular organic matter for C. crispus is known to produce large amounts (4.4 mg C·100 $g^{-1}·h^{-1}$, according to Sieburth 1969). These exudates can be autoinhibitory or inhibitory to other organisms and take part in the abundance control.

Unattached populations of C. crispus have been reported in different parts of the world: Denmark (Rosenvinge 1931; Austin 1960), Newfoundland (South and Hooper 1980), St. Pierre and Miquelon Islands (R.G. Hooper, pers. comm.), Prince Edward Island (L.A. Hanic,[2] pers. comm.), the USA (Moss cited by Prince and Kingsbury 1973b). They are found in landlocked seas, shallow inlets, quiet bays, or estuaries (Austin 1960) where currents are reduced. There, substrate seems not to be a limiting factor as plants lie on or near the sandy or muddy bottom in shallow waters. Algae are sterile, and multiplication occurs only by vegetative means (fragmentation). This can be considered as an adaptation to the absence of stable substrate for the settlement and development of spores (Austin 1960). Plants are devoided of holdfast organs and their shape is globular or subglobular, suited to rolling about on the sea bottom. Branching is often profuse.

Salinity does not seem to be a limiting factor in normal range. Numerous authors (Humm 1948; Marshall et al. 1949; Doty and Newhouse 1954; MacFarlane 1966; 1968; Lilly 1968; Mathieson et al. 1969; Mathieson and Burns 1971; 1975; Burns and Mathieson 1972; Bird et al. 1979) emphasized the euryhaline character of C. crispus as it tolerates salinities varying from 15‰ to 45‰ with an optimum near 30‰. Lilly (1968), with limited data, suggested, however, that the apparent preference of this alga to estuarine conditions is more likely due to a decrease in wave exposure than a reduction of salinity.

C. crispus is an eurythermic species (Montford et al. 1955; Newton et al. 1957; Newell and Pye 1968; Mathieson and Burns 1971; Burns and Mathieson 1972; Prince and Kingsbury 1973c; Bird et al. 1979; Simpson and Shacklock 1979; Braud and Delépine 1981). For example, in eastern Canada, it tolerates around -0.5°C in winter and over 20°C in summer. Temperature optimum varies, according to authors, between 15°C and 20°C; temperatures over 30°C are lethal.

C. crispus is also euryphotic as thalli occur either in shaded sites (under shelter of overhangs, in tide pools, under cover of other seaweeds as Fucales and Laminariales) or in full sunlight (Kanwisher 1966). However, seawater turbidity may be a factor in determining the lower limit of C. crispus distribution (Levring 1947; Mathieson and Burns 1975). Colouration varies from dark purple-red to yellow-greenish, according to depth (MacFarlane 1956) and season (MacFarlane 1968): this is partly the consequence of variations of incidental light intensity. Kylin (1912) and Rhee (1970) showed that lower shore forms contain less phycocyanin than upper level forms. They discussed the significance of this with regard to theories of "complementary chromatic adaptation" and "adaptation to light intensity" (Engelmann 1883; Oltmanns 1893; Harder 1923).

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[2]L.A. Hanic, Department of Biology, University of Prince Edward Island, Charlottetown, P.E.I. CIA 4P3, Canada

Biological competition for space is a determinant factor for distribution and abundance of populations (Mathieson and Prince 1973). Interspecific competition on European coasts occurs with the following macroalgae: Mastocarpus stellatus, Corallina officinalis, Laurentia pinnatifida, Fucus vesiculosus, Fucus serratus, and Ascophyllum nodosum. However, on eastern Canadian coasts, the following species, as well as the above, compete with C. crispus: Phyllophora sp.; Furcellaria fastigiata, Lithothamnion sp., Ahnfeltia plicata, Chordaria flabelliformis, and Cystoclonium purpureum (MacFarlane 1956; 1966).

Concerning animals, MacFarlane (1952; 1956; 1968), Lilly (1968), and Reynolds (1971) observed competition between C. crispus, Mytilus edulis, and Littorina littorea. The latter - as Gammarus oceanicus, Idotea baltica, and Lacuna vincta (Shacklock and Croft 1981) - restricts development of thalli by grazing. Skutch (1926) reported the amphipod Amphitoe rubricata as a herbivore feeding on C. crispus. The sea urchin Strongylocentrotus droebachiensis appears as a major grazer of C. crispus beds in New England and Canada (Lilly 1968; MacFarlane 1968; Pringle et al. 1980; Pringle 1986).

C. crispus is host to both epiphytes and epizoids which reduce both available light and commercial value (Lilly 1968). The occurrence of these organisms varies qualitatively and quantitatively according to their own life cycle. Among others, Darbishire (1902), Rosenvinge (1931), Bell and MacFarlane (1933), Fritsch (1945), Marshall et al. (1949), MacFarlane (1952; 1964; 1966; 1968), Taylor (1957-1958), Lamb and Zimmermann (1964), Lilly (1968), Prince (1971), Kopp (1975), and Pybus (1977) enumerated the epiphytic flora whose main species are given in Table 2. In the opinion of MacFarlane (1952; 1964) and Pybus (1977), the more the habitat is exposed, the less epiphytes are growing.

Lilly (1968) and Pringle and Semple (1976) gave detail lists of animals living on or among fronds of C. crispus. The species are generally small in size, but the spawn of larger animals have been observed (Echinodermata, Mollusca, Arthropoda). These tabulations mention over 75 taxa belonging to the following phyla: Porifera, Cnidaria, Platyhelminthes, Annelida, Arthropoda, Mollusca, Ectoprocta, Echinodermata, and Chordata. The Bryozoans Membranipora sp. and Electra pilosa, and the Polychaete Spirorbis borealis, are frequently attached, especially on subtidal thalli (Rogick and Croasdale 1949; Yonge 1949; MacFarlane 1952; Carson 1955; Lilly 1968; Prince 1971; Kopp 1975; Mathieson and Burns 1975).

H. LIFE CYCLE

1. Sexual reproduction

The sexual cycle of C. crispus has been described by numerous authors: Darbishire (1902), Kylin (1917; 1923), Rosenvinge (1931), Chemin (1937), Weber (1960), MacFarlane (1968), Ring (1970), Prince (1971), Chen and McLachlan (1972), Prince and Kingsbury (1973a), and Taylor and Chen (1973). Chen and McLachlan (1972) were the first to complete it in culture.

Table 2. Epiphytic flora on Chondrus crispus Stackhouse.

Class	Sub-Class	Order	Family	Genus and Species
Rhodophyceae	Bangioideae	Bangiales	Bangiaceae	Porphyra sp.
	Florideae	Acrochaetiales	Acrochaetiaceae	Acrochaetium sp.
		Cryptonemiales	Corallinaceae	Melobesia sp. Dermatolithon pustulatum Corallina officinalis
		Gigartinales	Furcellariaceae	Furcellaria fastigiata
			Rhodophyllidaceae	Cystoclonium purpureum
			Gracilariaceae	Gracilaria verrucosa
		Rhodymeniales	Rhodymeniaceae	Palmaria palmata
			Champiaceae	Lomentaria articulata
		Bonnemaisoniales	Bonnemaisoniaceae	Bonnemaisonia hamifera (Trailliella intricata)
		Ceramiales	Ceramiaceae	Ceramium sp. Spermothamnion repens
			Delesseriaceae	Nitophyllum sp.
			Rhodomelaceae	Brongniartella byssoides Polysiphonia sp. Laurencia sp.
Phaeophyceae	Phaeosporeae	Sphacelariales	Sphacelariaceae	Sphacelaria cirrosa
		Chordariales	Corynophlaeaceae	Corynophlaea crispa Leathesia difformis
			Chordariaceae	Chordaria flabelliformis
		Laminariales	Laminariaceae	Laminaria sp.
	Cyclosporeae	Fucales	Fucaceae	Fucus sp.
			Himanthaliaceae	Himanthalia elongata
Chlorophyceae	Septophycideae	Ulvales	Monostromaceae	Monostroma sp.
			Ulvaceae	Ulva sp. Enteromorpha sp.
	Siphonophycideae	Cladophorales	Cladophoraceae	Rhizoclonium tortuosum Chaetomorpha sp. Spongomorpha spinescens Cladophora sp.

A Polysiphonia-type life history has been demonstrated (haplodiplophasic isomorphic trigenetic cycle). There is a succession of: 1) a haploid and diocious (separate males and females) gametophytic generation; 2) a diploid carposporophytic generation, which is a parasite of the female gametophyte; and 3) a diploid tetrasporophytic generation, whose morphology is similar to the first generation (Fig. 3).

Carpospores depart through convex surfaces of carposporangial sori; the mechanism for release is still not yet understood (Taylor and Chen 1973). They give rise to tetrasporophytic thalli. Ring (1970) showed that germination can be either semi-filamentous (rhizoids) or discoid, and suggested that the occurrence either of one or the other of these depends on spore density. West (1972) demonstrated for Mastocarpus (alternation of the phases Gigartina and Petrocelis) that the factor controlling the germination is the type of initial contact by the spore with the substratum and that it does not influence later the morphology of the erect part of the thallus. According to Chen and Taylor (1976), the formation of a blanket-like extracellular sheath, preceding internal cell differentiation, leads to the discoid-type development; its failure would permit the disorganized outgrowth of the rhizoid-like filaments. The erect frond develops from a single large cell which at first is cylindrical and then more or less flattened. The manner in which the structure becomes multiaxial is still in doubt (Taylor and Chen 1973).

Tetrasporophytes become recognizably distinct when they are mature and bear sori of cruciated tetrasporangia located in the medulla (Harvey 1846-1851; Darbishire 1902; Kylin 1923; 1956; Rosenvinge 1931). They appear as spots, sometimes confluent, dark-red (or white when they are empty), in the distal portion of a frond. They are slightly swollen on both sides. Mature tetraspores are released, as a ribbon-like extrusion in a sticky matrix (Prince and Kingsbury 1973a), through one to three pores in the sorus surface. Chen and McLachlan (1972) showed that tetraspore germination, initiation of erect fronds, and development are similar to that of carpospores.

Female gametophytes are morphologically recognizable only when they bear carposporophytes. The development of the procarp in C. crispus has been described by Schmitz (1883), Darbishire (1902), and Kylin (1923). A large cell, the auxiliary cell, forms a three-celled carpogonial branch within the inner cortex near the apical parts of the frond. Prince (1971) noted 80 procarps in a single ramification. Fertilization and fusion of the carpogonial branch with the auxiliary cell occur. Then, the procarp produces gonimoblast filaments in the medulla. They give rise to numerous carposporangia. The latter are regrouped in dark-red sori prominent on one side of the frond: the carposporophytes.

Male gametophytes are difficult to distinguish morphologically. They tend to have less branches and be more subcylindrical at the apex than female plants. Development and phenology of spermatangia have been described by Buffham (1896), Darbishire (1902), Grubb (1925), Marshall et al. (1949), Chen and McLachlan (1972), Mathieson and Prince (1973), and Taylor and Chen (1973). Sori of spermatangia appear as whitish or pale-pink zones located in the terminal 3 to 10 mm of apices; but this cannot constitute a criterion of

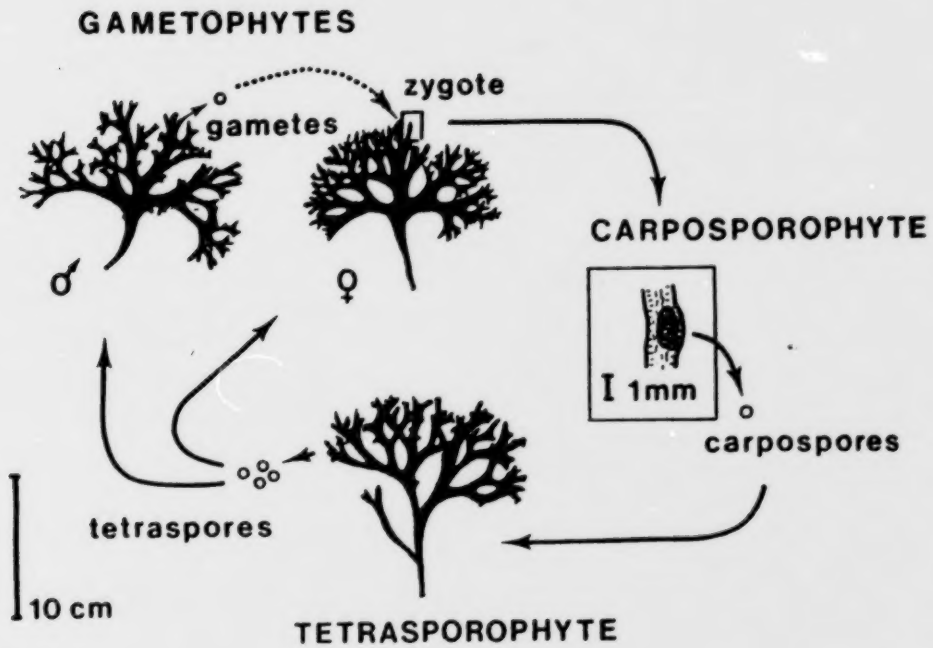

Figure 3. Reproductive cycle of Chondrus crispus Stackhouse [diagram by Floc'h (1982)].

determination because tips of vegetative plants have also this colour during periods of active growth (Hanic 1973); the only way is then to have recourse to miscroscopic study.

It was probably this difficulty of observation with the naked eye that gave rise to the opinion that male gametophytes were rare (Rosenvinge 1931; Marshall et al. 1949; Prince and Kingsbury 1973a) or non-existent (Prince 1971). Consequently, other types of reproduction were mentioned as parthenogenesis (Prince and Kingsbury 1973a), syndiploidy (Hanic 1973), or apomixy (Chen 1977). However, Tveter-Gallagher et al. (1980), from a study with electronic microscopy, were able to accurately describe the spermatangia development and showed that male gametophytes can represent up to 21% of a population and have a wide geographic distribution along the northwest Atlantic coasts. True sexual reproduction should no longer be questioned. Spermatia have never been observed attached to trichogynes protruding through the cuticle, nor fertilizing carpogonia. As well, nuclear fusion has not been observed between the latter and auxiliary cells. However, culture experiments by Chen and McLachlan (1972) and Chen and Taylor (1980b) showed that male gametophytes had to be present in the same culture to permit the formation of carposporophytes. Studies of Magne (1964) and Hanic (1973) support fertilization; they both noted meiosis and found gametophytes to be haploid and tetrasporophytes to be diploid.

Other ways of reproduction, besides vegetative propagation, should not be disregarded. Anomalies in other red seaweeds have been previously mentioned (Isaac and Simons 1954; West and Norris 1966; van der Meer and Todd 1977; West and Hommersand 1981). Concerning C. crispus, two phenomena, still unexplained, have been described:

- small mature tetrasporophytic fronds growing on a female gametophytic thallus (Tveter-Gallagher and Mathieson 1980);

- male plants producing large masses of spores (van der Meer et al. 1983).

2. Vegetative reproduction

This reproductive mode is well known in C. crispus and allows both harvesting and aquaculture (Neish and Fox 1971; Neish et al. 1977). Every part of the thallus (cortex or medulla either apical or from the basal disc) has the potential to regenerate new fronds (Chen and McLachlan 1972; Chen and Taylor 1978). The more significant regrowths arise from holdfasts; thus one can maintain populations if care is taken not to destroy the latter (Marshall et al. 1949; MacFarlane 1968; Taylor 1970).

I. DISTRIBUTION OF THE DIFFERENT GENERATIONS AND REPRODUCTIVE PERIODS

One of the main problems in determining the distribution of life-cycle phases is that the gametophytic and tetrasporophytic thalli are isomorphic. Distinction in most of the studies was made only when plants were mature,

which brought unavoidably a bias in the determination of these periods, the proportion of "vegetative plants" being overestimated. The method of Craigie and Leigh (1978) consisting of determining which fraction of carrageenan is present in specimens [κ for gametophytes and λ for tetrasporophytes (McCandless et al. 1973)] allows a more precise approach. The only known study using it is that of Craigie and Pringle (1978).

Prince and Kingsbury (1973b), when assessing reproductive phenology, recommended not only to consider the presence or absence of sori, but also the following: age and maturity of sori, appearance or lack of carpogonia, viability of spores in the sorus, degree of mycological infestation of the sorus, number of sori able to release spores in laboratory, viability of the released spores, proportion of full or empty sori, and number of spores in the water column. Thus, the carpospore abundance observed in February-March is actually, according to these authors, an artifact in terms of effective reproduction because, at this time of the year, many sori are empty or full of non-viable spores. Some plants are able to release spores continuously over many months. Ring (1970) mentioned a specimen which released carpospores over 4 mo. Chen and McLachlan (1972) reported a similar observation for spermatia from a male gametophyte in vitro.

Mathieson and Burns (1975) and Craigie and Pringle (1978) found that distribution of life-cycle phases varies with depth: tetrasporophytic thalli are more abundant in the outer portions of the beds in deeper water. Studies of Craigie and Pringle (1978), Wright (1981), and Bhattacharya (1985) showed, in Prince Edward Island and Nova Scotia, Canada, a gametophytic dominance except at one location on the north shore of Nova Scotia (Toney River). This dominance cannot be explained by more significant survivorship or spore release. The haploid phase seems to be more competitive than the diploid phase regarding recruitment, and has a superior frond growth rate (Bhattacharya 1985). Chopin (1985) noticed in Brittany, France, that, except for the beginning of winter and middle of autumn, tetrasporophytes are always less abundant than gametophytes whatever the bathymetric level. They are two times more frequent at the sublittoral level than at the mediolittoral. Differentiated plants are, generally, more abundant at the first level than at the second.

Studies on reproductive periods of C. crispus are numerous and sometimes in opposition (Fig. 4). In spite of geographical variations, they suggested that generally reproduction takes place all year long with maxima in summer and autumn for female and male gametophytes, and from autumn to spring for tetrasporophytes. The fact that the three generations can be observed throughout the year suggests that the sexual cycle is not controlled only by environmental parameters (Chen and McLachlan 1972).

According to Tveter-Gallagher et al. (1980), the reproductive period is shorter and later for seaweeds at the upper limit of the vertical zonation. This could be explained by a more significant pressure of environmental factors at this level (Zaneveld 1969). In other respects, female plants bearing carposporangial sori have a unimodal periodicity (autumn) for

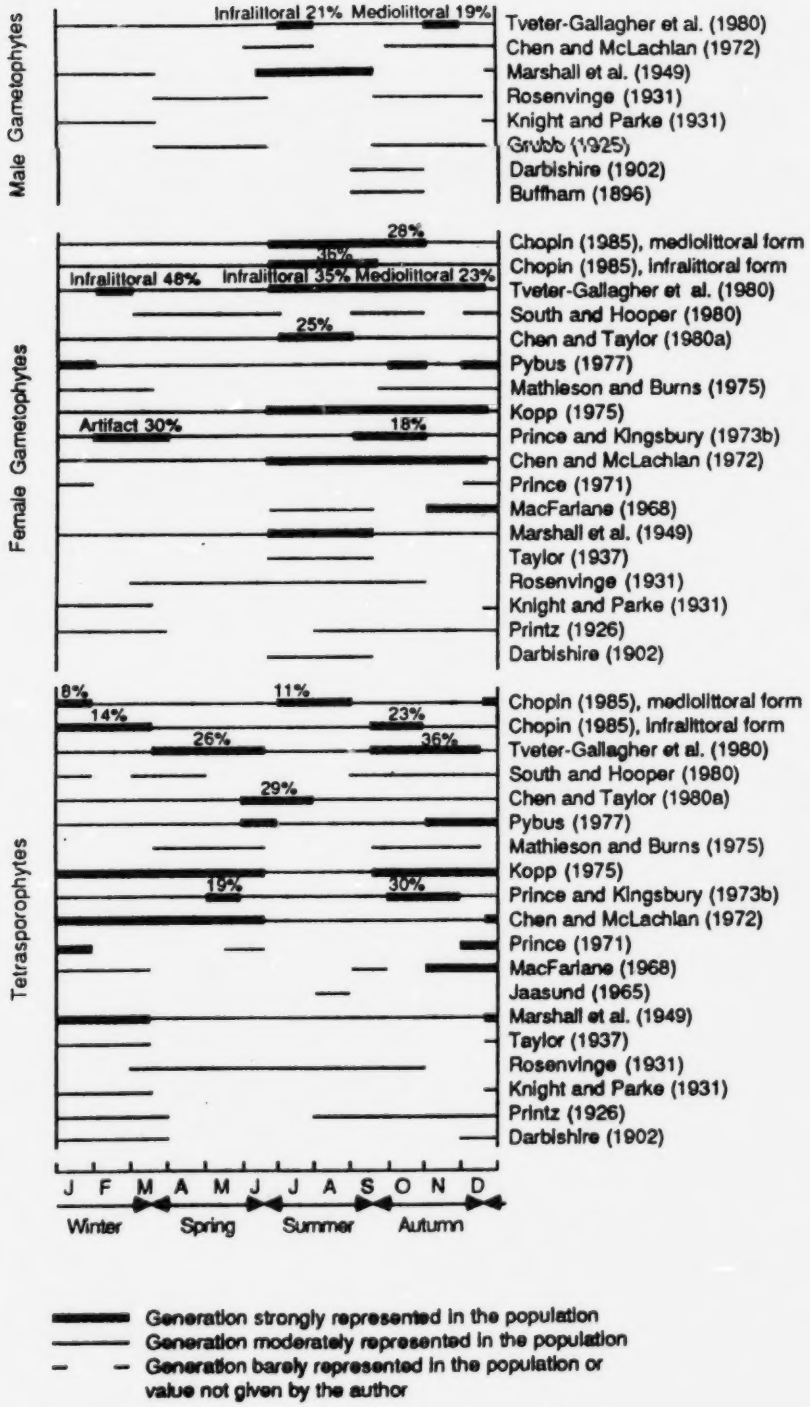

Figure 4. Distribution of the different generations during the year and reproductive periods in Chondrus crispus. Percentages show the portion of fructified plants of the generation in the population.

mediolittoral populations and bimodal (winter and autumn) for infralittoral ones which, moreover, have more mature females. Finally, at some locations, male gametophytes are more abundant at the infralittoral level than at the mediolittoral and their reproductive maxima are shifted: August for infralittoral, November for mediolittoral.

Chopin (1985) demonstrated that fertile female gametophytes have a maximal abundance in summer in the infralittoral and in summer-early autumn in the mediolittoral. This phase is represented at its minimum in winter. Distribution of differentiated tetrasporophytes shows two maxima in abundance per year. They appear earlier in the mediolittoral form (beginning of winter, summer) than in the infralittoral (winter, beginning of autumn). Minima are observed in the middle of autumn and during spring. For both gametophytes and tetrasporophytes, the pattern is more contrasted at the sublittoral level, contrary to the results of Tveter-Gallagher et al. (1980). Chopin (1985) suggested that environmental conditions in the mediolittoral vary seasonally more significantly than in the infralittoral. They create, then, a much less stable habitat and are much less favourable to the preferential development of one of the two generations. In the infralittoral form, summer maximum of gametophytes seems to be intercalated between the two maxima of tetrasporophytes (winter, beginning of autumn). This could be explained by alternation of generations in the reproductive cycle of this species. However, in the mediolittoral form, this pattern is not observed: in summer, the two sexual phases are strongly represented.

J. PERIODS OF GROWTH

Numerous authors have studied the growth of C. crispus (Fig. 5). It appears that generally it is significant during spring and summer and minimal during winter. Causes of shifts in the optima seem to be essentially related to the environmental conditions peculiar to each study site and to the chosen mode of expressing the results (growth in length: $mm \cdot d^{-1}$; growth in surface: $mm^2 \cdot mm^{-2} \cdot d^{-1}$; growth in biomass: $gFW \cdot cm^{-2}$; growth in number of cortical cell rows neo-formed).

Chopin and Floc'h (1987) perfected a cytological method to estimate algal tissue growth using the cellufluor fluorescent dye technique. They showed that growth is not only terminal, contrary to what is conventionally accepted in multiaxial, cladomial structured algae (Chadefaud 1960; Chen and McLachlan 1972), but that it is extended to at least the upper half of the thallus. In fact, the middle of the latter is an active growth area where it probably induces an enlarging and a thickening of the alga. The thallus base shows no growth. Besides, they observed seasonal variations of growth: slow at the beginning of spring; increasing toward the end of spring; slowing down at the beginning of summer; and increasing again to reach a maximum in autumn. Growth is minimal during winter. In other respects, the growth rate by thickness and length is more significant in the infralittoral form than in the mediolittoral. This might explain in part the morphological and size differences that one can observe in the adult plants of these two forms.

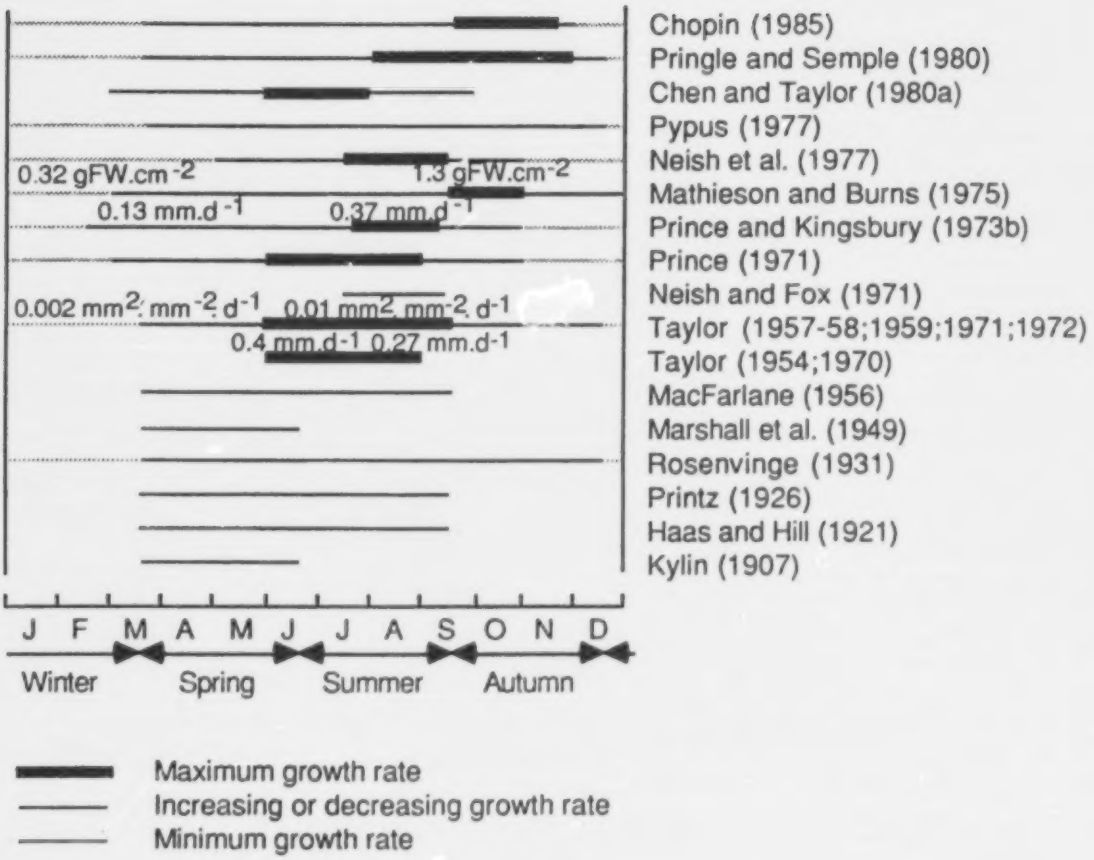

Figure 5. Periods of growth during the year in Chondrus crispus.

None of the authors mentioned in Figure 5 have attempted to distinguish growth between the gametophytic and tetrasporophytic generations. According to Chen and McLachlan (1972) and Kopp and Pérez (1978), it is anyway independant of sexual potentiality and maturity. Pybus (1977) found growth ceases when plants reach maturity. Neish (1972) and Kopp and Pérez (1978) underlined a strong individual variability.

Taylor (1954; 1972) described slow growth for C. crispus; the rate (increase per surface unit in $mm^2 \cdot mm^{-2} \cdot d^{-1}$) was of the same order for both young and old fronds. Hydrographic and bathymetric conditions had no influence on growth. Kanwisher (1966) suggested thallus doubling (stage not given) in 6 to 9 d. Prince and Kingsbury (1973b) observed that germlings are able to double their surface area in 8 to 9 d. Pybus (1977) found a continuous growth throughout the year with a slight reduction during the winter months.

Using the classification of Taylor (1970), Prince and Kingsbury (1973b), Mathieson and Burns (1975), and Pringle and Semple (1980) studied growth of four classes of fronds:

- Class I: unbranched;
- Class II: two to few branches or much branched but not over 6 cm tall;
- Class III: much branched, 6 to 10 cm tall;
- Class IV: branched, over 10 cm tall.

The pattern of these different classes follows that of growth. For Mathieson and Burns (1975), the strongest proportion of tall plants and the most significant biomass are observed from August to October, the minimum being in winter.

To suppress the heterogeneity of Class III observed by G.J. Sharp[3] (pers. comm.), Chopin and Pringle work presently with a five-class system:

- Class I: unbranched;
- Class II: up to three dichotomies whatever the height, or less than or equal to 6 cm tall whatever the number of dichotomies;
- Class III: four or five dichotomies, 6 to 10 cm tall;
- Class IV: more than five dichotomies; 6 to 10 cm tall;
- Class V: over 10 cm tall whatever the number of dichotomies.

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[3]G.J. Sharp, Biological Sciences Branch, Scotia-Fundy Region, Department of Fisheries and Oceans, Halifax, N.S. B3J 2S7, Canada

Ehrke (1931), Mathieson and Burns (1971; 1975), Prince (1971), Burns and Mathieson (1972), Taylor (1972), and Neish et al. (1977) observed that growth variations of C. crispus are closely related to seawater temperature: the beginning of growth in spring and the maximum at the end of summer-beginning of autumn coincide respectively with the increase and the maximum of water temperature. Pybus (1977) noticed that air temperature may also influence growth of eulittoral fronds. Neish and Fox (1971) reported a maximal growth from mid-July to mid-September. Before this time, when photoperiod is maximal, the limiting factor appeared to be reduced water temperature. After September, the decrease of the growth rate may be attributable, not to seawater temperature which is still high, but this time to the diminishing photoperiod.

In other respects, it has been shown for many seaweeds (for review: Gagné et al. 1982; Rosenberg and Ramus 1982), that variations of nutrient concentrations in seawater may influence growth; this is likely the case for C. crispus. For example, Mathieson and Burns (1975) showed that growth increases at the beginning of spring and reaches its maximum in summer with nutrient concentration maximized and minimized respectively. Prince and Kingsbury (1973b) suggested that ammonium ions may serve as a nitrogen source as C. crispus active growth period coincided with low nitrate concentrations but abundant ammonium ions. Neish et al. (1977) showed that the addition of either of these elements leads to a stimulation of growth.

Chopin (1985), in his study of phosphorus nutrition, carrageenans, and growth, showed that their variations were interrelated and under close control of external parameters such as photoperiod, and seawater temperature and nutrient concentration (Table 3).

The slow growth, at the beginning of spring, in spite of abundances of phosphates and nitrogen in seawater, may be ascribed to reduced photoperiod and low temperatures. This corroborates the results of Mathieson and Burns (1975), Gordon et al. (1981), and Gagné et al. (1982). Consequently, one can agree with Black and Dewar (1949) and Gagné et al. (1982) that since the photosynthetic activity does not provide enough energy to give rise to the observed growth, the alga must draw on its carbonate reserves. This hypothesis suggests that the intermediate compounds of the photosynthetic cycle are oxidized, thus preventing the carbohydrates, such as carrageenans, from accumulating in tissues. Carrageenans are at a minimum at this time of the year.

Longer days and higher temperatures, at the end of spring, promote growth. This has also been observed by Mathieson and Burns (1975), Neish et al. (1977), and Fortes and Lüning (1980). Seawater, at this time, is low in nutrients; hence, growth can be carried out only at the expense of phosphorus and nitrogen reserves formed by the alga during winter. This hypothesis renders an account of the shift observed between the decline of phosphorus content in the alga and in seawater. It is consistent with the results of Birch et al. (1981), Gordon et al. (1981), Gagné et al. (1982), Kornfeldt (1982), and Rosenberg and Ramus (1982). Moreover, study of the pattern of phosphorylated compounds in the thallus of C. crispus suggests that hydrosoluble organic and acido-insoluble fractions might be reserve pools of

Table 3. Seasonal variations of main environmental factors, phosphorus nutrition, carrageenans, and growth in Chondrus crispus. ↗ increase; ↘ decrease.

	Beginning of spring	End of spring	Beginning of summer	End of summer	Autumn	Winter
Light duration in photoperiod	low	↗	maximum	↘	↘	minimum
Seawater temperature	low	↗	↗	maximum	↘	minimum
Phosphorus (and nitrogen) concentration in seawater	high, but beginning to decrease	↘	minimum	↗	↗	maximum
Phosphorus (and nitrogen) content in the alga	maximum	↘	minimum	↗	↗	high
Total carrageenan content	minimum	↗	average	↗	maximum	↘
Growth	low	↗	↘	↗	maximum	↘ minimum

phosphorus and be used in spring by the alga. If this hypothesis is verified, this would mean that phosphorus storage is done in a different way in seaweeds to that of higher plants. It is conventionally accepted in the latter that it is the inorganic fraction, distributed in several cellular compartments, which plays the role of a reserve pool (Bieleski 1973; Roberts et al. 1984). The manner of using stored phosphorus would also be different from that of nitrogen, for which it is recognized that seaweeds use first inorganic forms before organic ones (Chapman and Craigie 1977; Gagné et al. 1982).

The reduction in growth, at the beginning of summer, can be explained by shortages of phosphorus and nitrogen reserves. These reserves cannot be replenished because seawater nutrient concentrations are minimal. At the end of summer, recovery of growth seems to be due to the regeneration of nutrients in seawater and their accumulation in the alga again.

The growth of C. crispus is at its maximum in autumn. This result seems not to be attributable to one or the other of the studied factors, because none of them are optimal at this season. It may, however, be due to synergy between them. As a matter of fact, if the length of days is similar to that in spring, seawater temperature is higher and phosphorus content increases both in seawater and in the alga. Besides, it appears that the slow down of growth in summer prevents C. crispus from exhausting its carbohydrate storage. Thus, contrary to what happens in Laminariales (Black and Dewar 1949; Chapman and Craigie 1977), the synthesis of carbohydrates is able to continue and the latter can accumulate, particularly in the form of carrageenans, whose content is at its maximum in autumn.

In winter, it seems that the limiting factors of growth are above all photoperiod and seawater temperature as shown by Neish and Fox (1971), Taylor (1972), and Mathieson and Burns (1975).

K. LONGEVITY

Holdfasts and erect fronds of C. crispus are perennial (Darbishire 1902; Printz 1926; Rosenvinge 1931; Thomas 1938; Taylor 1959-1960; 1972; Mathieson and Burns 1975; Craigie and Pringle 1978). If one refers to the biological type nomenclature of marine seaweeds of Feldmann (1951), it is a species belonging to the group of Phanerophyceae.

According to Rosenvinge (1931), Marshall et al. (1949), and Taylor (1959-1960), erect fronds grow generally during 2 to 3 yr. MacFarlane (1968) estimated longevity at 4 to 5 yr. Although the latter author thought that plant reproductive maturation takes place 5 yr after spore germination, Rosenvinge (1931), Taylor (1959-1960), Pybus (1977), and Pringle and Semple (1980) showed that it can take place in 2 to 3 yr-old thalli.

The longevity of holdfasts is not well known (Ring 1970). Taylor et al. (1981) reported to have seen holdfasts continuing to increase in area over a 4 yr period. Regular growth layers developed in holdfasts of cultivated C. crispus (Taylor et al. 1981). Rosenvinge (1931) and Marshall et al. (1949) observed two to three seasonal growth layers on specimens originating

in natural populations. However, the process of growth layer initiation is still in doubt, and seems to be associated with frond formation (Rosenvinge 1931) and growth (Taylor et al. 1981).

II. CARRAGEENANS

Among compounds presently extracted from seaweeds, cell-wall polysaccharides have the highest commercial value (Bidwell 1982). They are called carrageenans in C. crispus. However, our knowledge, up to the present day, of their biochemistry and biophysics still does not allow us to rigorously define parameters which control their synthesis and properties, particularly with respect to gelling, thickening, stabilizing, binding, bodying, suspending, precipitating, clarifying, and filming aspects which are so much used by industry.

At this point, we will recall acquired results on architectural organization, eco-physiological role, and seasonal variations of carrageenans. We will also dedicate a section to their utilization.

A. ARCHITECTURAL ORGANIZATION OF CARRAGEENANS

1. The cell wall of algae

The algal cell wall is composed of two distinct regions: first, the sensu stricto cell wall (or immediate cell wall as used by Gordon and McCandless 1973; Gordon-Mills and McCandless 1975; Callow and Evans 1976), which is a thick succession of stratified rows around each cell; secondly, the intercellular matrix, which is an apparently amorphous substance between adjacent cells.

The cell wall has also been thought of as a biphasic system where a crystalline phase, the microfibrillar phase, is dispersed in a continuous, amorphous or pseudo-crystalline phase, the matrix.

2. Organization of the microfibrillar phase

The most widely distributed microfibrillar compound is cellulose, a polymer of β-1,4-D-glucose (Kreger 1962). But, in contrast to terrestrial plants which can contain up to 30% of their dry weight in cellulose (Preston 1974), rhodophytes have low cellulose concentrations varying from 1 to 8% (Ross 1953). Cellulose values reported for C. crispus are as follows:

- Church (1876)	2.15% DW
- Russell-Wells (1922)	2.20% DW
- Ross (1953)	2.00% DW
- Young (1966; 1969)	0.44% DW
- Percival and McDowell (1967)	2.00% DW
- McCandless et al. (1977)	0.00% DW

Cell-wall microfibrils are arranged in lamella, tangential to the cell surface. In each lamellar plane, microfibrils are tangled up in a more or less loose network and show a strong angular dispersion (Myers and Preston 1959).

Hanic and Craigie (1969) showed that the cuticle of two chlorophycean (Cladophora rupestris and Chaetomorpha melagonium), one phaeophycean (Padina vickersiae), and one rhodophycean (Porphyra umbilicalis) marine algae is composed of alternate microfibrillar and amorphous protein-rich layers similar in appearance to those seen in innermost carbohydrate-rich regions.

3. Organization of the matricial phase

The study of matricial polyosides is more recent than that of microfibrillar polyosides. The resurgence of works devoted to them has been promoted by the display of their abundance [up to 76% DW in C. crispus according to Fuller and Mathieson (1972)] and their industrial interest (Kloareg 1982).

Research on carrageenans may be divided into four periods (Yaphe 1973). First, up to 1950, showed that carrageenans contained sulphated D-galactose, and that, after addition of potassium chloride, they form a thermoreversible gel similar to the one obtained with agar. During the second phase (1952-1960), the difference in chemical structure between agar and carrageenans was determined. O'Neill (1955) showed that 3,6-anhydro-D galactose was a major residue in the latter. Smith and Cook (1953) divided carrageenans into two families on the basis of solubility differences in potassium chloride: κ-carrageenans are insoluble while λ-carrageenans are soluble. The third period, between 1960-1969, was dominated by the works of Rees and co-workers (Rees 1969b) who based the carrageenan nomenclature on the number and position of ester-sulphuryl groups on galactose. The fourth period is present research and mainly consists of physico-chemical studies of carrageenans through the following methods:

- chemical analysis of the main constituents as total carbohydrates, galactose, anhydro-galactose and sulphates (Craigie and Leigh 1978);
- immunological methods (Hosford and McCandless 1975; Gordon-Mills and McCandless 1975; Di Ninno and McCandless 1978a and b; 1979);
- enzymatic methods (Weigl and Yaphe 1966; Johnston and McCandless 1973; Bellion et al. 1981; 1982);
- spectroscopic methods:
  - infra-red (Anderson et al. 1968; Stancioff and Stanley 1969),
  - ^{13}C nuclear magnetic resonance (Yarotsky et al. 1977; Bhattacharjee et al. 1978a; Usov et al. 1980; Rochas et al. 1980; Bellion 1982; Bellion et al. 1983).

3.1. Primary structure of carrageenans. Since the works of Rees and collaborators in England (Rees 1963; Dolan and Rees 1965; Anderson et al. 1973; Penman and Rees 1973a, b, and c), it is established that carrageenans are formed from a regular repetition of the same basic diosidic figure (AB) of two unities of galactose alternatively linked by bindings β(1→4) and α(1→3). Polyoside may then be considered as an homopolymer with β-D-galactopyranosyl(1→4)α-galactose as monomer, itself linked in 1 and 3 (Rees 1969a and b). This structure may be masked by various substitutions (ester-sulphuryl, methoxyl, or pyruvate) but always comprises D-galactose linked in (1→3) as subjacent B unities.

The κ-carrageenan family consists of polymers with 4-sulphate-β-D-galactopyranosyl(1→4)α-D-galactose basic figure. They are κ-, ι-, μ-, and ν-carrageenan whose A unities are respectively 3,6-anhydro-α-D-galactose, 3,6-anhydro-α-D-galactose-2-sulphate, α-D-galactose-6-sulphate, and α-D-galactose-2,6-disulphate. Moreover, Penman and Rees (1973c), Lawson et al. (1973), Santos and Doty (1975), and Dawes et al. (1977) showed the occurrence of deviant ι-carrageenan in which the A unity would be formed of α-D-galactose-2-sulphate.

Lawson and Rees (1970) and Wong and Craigie (1978) having isolated, from fresh seaweeds, an enzyme able to eliminate sulphate of α-D-galactose-6-sulphate to convert it in 3,6-anhydro-α-D-galactose, μ- and ν-carrageenans have been defined as biological precursors of κ- and ι-carrageenans respectively. An alkaline process leads to the same transformation (Percival and McDowell 1967).

The works of Bellion (1982) and Bellion et al. (1982; 1983) showed that κ- and ι-carrageenans have no pure κ- or ι-structures, but appear to be κ/ι hybrid molecules with respectively κ- or ι-dominant features. If one also considers the works of Black et al. (1965), Anderson et al. (1968), Stancioff and Stanley (1969), Hirase and Watanabe (1972), Lawson et al. (1973), Penman and Rees (1973a), Santos and Doty (1975), Bhattacharjee et al. (1978b), Chopin (1985), essentially on the genera Mastocarpus, Eucheuma, Ahnfeltia, and Chondrus and which showed also κ/ι hybrids containing μ- and ν-residues, it leads to the assumption that the biosynthetic pathways of κ- and ι-carrageenans could be similar or at least have a common first step (Di Ninno and McCandless 1979; Bodeau-Bellion 1983).

Carrageenans of the λ-family were defined by Rees (1969a and b) as those without 4-sulphate-β-D-galactose and 3,6-anhydro-α-D-galactose. These polymers are formed by a regular repetition of the figure 2-sulphate-β-D-galactopyranosyl(1→4)α-D-galactose-2,6-disulphate. Nevertheless, sulphate in 2 on β-D-galactose can be sometimes replaced by H. Lawson et al. (1973) and Penman and Rees (1973a and b) defined another member of the λ-family: ξ-carrageenan formed of 2-sulphate-β-D-galactopyranosyl(1→4)α-D-galactose-2-sulphate. Hirase and Watanabe (1972) showed the occurrence of π-carrageenan whose structure is derived from the former molecule by formation of a ketal cycle 4,6-O-(1-carboxyethylidene-D-galactose) with pyruvic acid substituted on B unity.

Recently, Greer and Yaphe (1984) defined the β-family including carrageenans whose A unity is formed from non sulphated α-D-galactose: the β-carrageenan [β-D-galactopyranosyl(1→4)3,6 anhydro-α-D-galactose] and its precursor the ϒ-carrageenan [β-D-galactopyranosyl(1→4)α-D-galactose-6-sulfate].

Haworth and conformational structures of main carrageenans mentioned above are given in Figure 6. Actually, mucilages extracted from carrageenophytes present themselves as a continuous spectrum of polydispersed macromolecules. Structures described formerly have therefore to be understood as idealized patterns of borderline polyosides and extracted carrageenan as a varied mixture of these borderline polyosides and intermediate structures (Stanley 1972).

3.2. Biochemical alternation of generations in the matricial phase. Although the idea was put forward as early as 1949 by Marshall et al. that variations in proportions of the different types of carrageenans might exist between gametophytes and tetrasporophytes of C. crispus, more than 20 yr passed before it was revived and studied thoroughly, particularly by McCandless and co-workers.

Thus, the works of McCandless and Richer (1972), Chen et al. (1973), McCandless et al. (1973; 1975), Pickmere et al. (1973), Gordon-Mills and McCandless (1975), Hosford and McCandless (1975), McCandless (1978; 1981), and McCandless et al. (1981; 1982; 1983) showed that, not only in C. crispus, but also in other Gigartinaceae and some Phyllophoraceae, male and female gametophytes elaborate carrageenans of the κ-family, whereas tetrasporophytes produce ones of the λ-family. This phenomenon, corroborated by immunochemistry (Di Ninno and McCandless 1978a and b; 1979), applies to species with either isomorphous or heteromorphous cycles (McCandless 1978).

Van der Meer et al. (1983), following observation in C. crispus of male plants bearing large masses of spores that gave rise in all probability to haploid tetrasporophytes, expressed the hypothesis that λ-carrageenan is bound to tetrasporophytic phenotype and not to nuclear phase (chromosomic ploidy) as tetrasporophytes, either diploid or haploid, produce this type of polyoside.

3.3. Significance of the cell-wall chemical composition in the taxonomy of seaweeds. Algal classification is based essentially on the following criteria: pigment type, storage substances, cell structure, reproduction, and morphology (Bold and Wynne 1978). The biochemical criterion, widely used in microbiology (Heywood 1966), is rarely used in phycology (McCandless 1978). Stoloff and Silva (1957) and Yaphe (1959) tried to correlate the nature of rhodophycean polyosides constituting algal cell walls with their taxonomic position. The idea was followed up by Percival (1978) and McCandless (1978). The latter underlined the complexity of this problem, particularly in the Phyllophoraceae. For example, in the genus Ahnfeltia, two species are carrageenophytes, A. durvillaei (Stancioff and Stanley 1969;

Haworth structure

Conformational structure

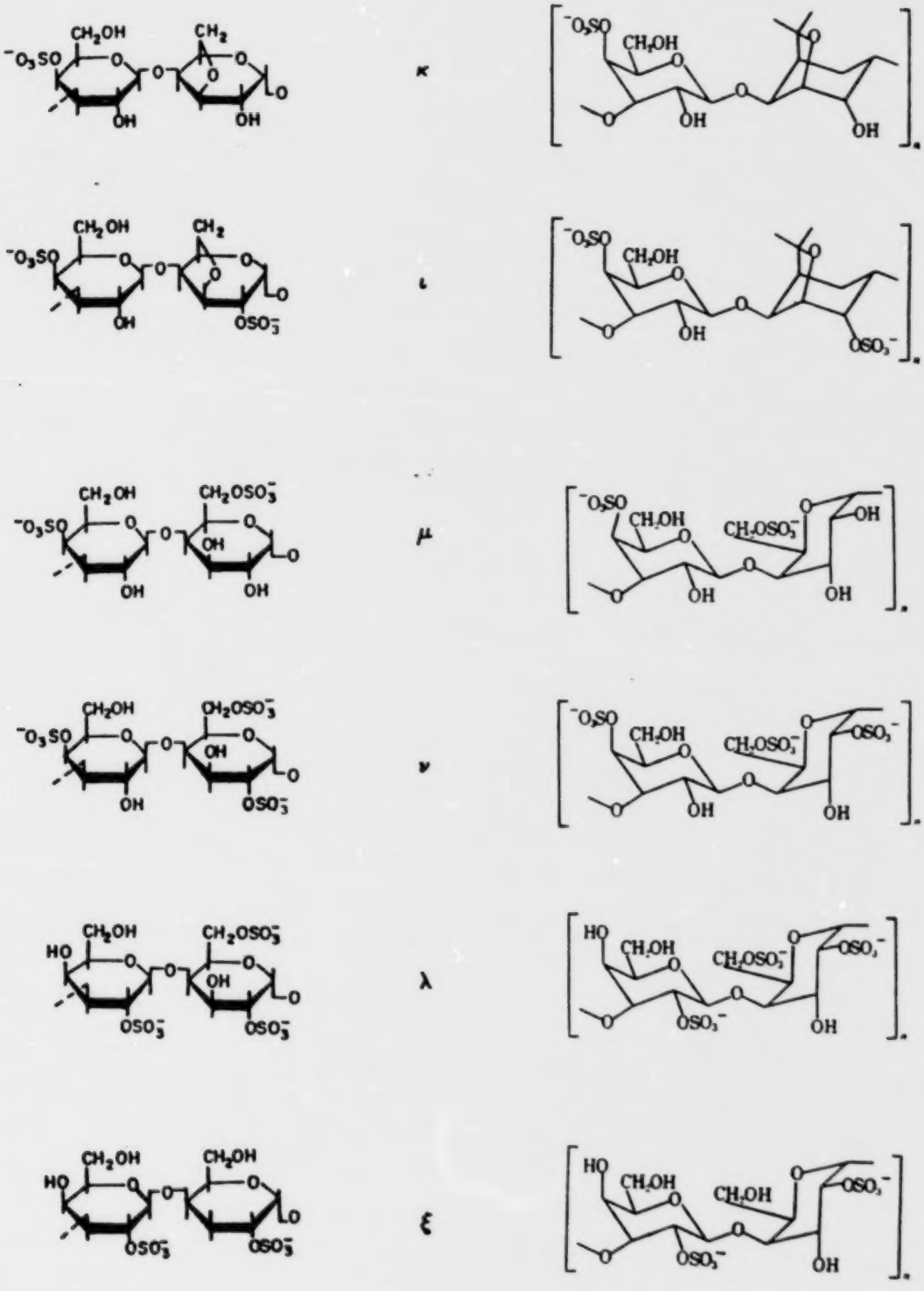

Figure 6. Structures of basic diosidic figure of main carrageenans.

Penman and Rees 1973a), and A. concinna (Santos and Doty 1975; Bhattacharjee et al. 1978b), but A. plicata is an agarophyte (Yaphe 1959; Bhattacharjee et al. 1978b).

Integration of the biochemical component in the classification of the red seaweeds seems to be an interesting approach even if, as pointed out by McCandless (1978),

> "...division on the basis of the constituent polysaccharides is either a taxonomist's nightmare, if one looks at the changes in classification which would have to result, or a biochemist's nightmare, if one looks at the existing classification and considers the analyses still to be done."

3.4. Secondary and tertiary structure of carrageenans. Variations in primary structure are responsible for the physico-chemical and biological properties of these polyosides in solution and especially for the structures of higher order: secondary, tertiary, and quaternary.

Conformations can be reduced to two types: ordered, or helices, and non ordered, or coils (Rees 1975). The in vivo structure of the algal matrix is often one of an intermediate semi-solid, semi-liquid system (Kloareg 1984). In very diluted solutions (polymer concentration lower than 1%), carrageenans take up a non-ordered conformation. Analysis of the ordered conformation shows that the comprehensive shape of λ-carrageenan is one of a very drawn-out helix with two disaccharide residues per step of 16.4 Å (Rees 1969a). In the case of κ- and ι-carrageenans, this ribbon-like conformation coils round itself owing to twisting imposed on the glucidic cycle by the 3,6-anhydro-galactose bridge (Rees 1972; Yaphe and Duckworth 1972). Comprehensive geometry of these two polymers is then the one of a straight helix with a 3:1 symmetry whose step is 24.6 Å for κ- and 26.0 Å for ι-carrageenan (Anderson et al. 1968; Rees 1969a).

3.5. Sol-gel transitions in carrageenans. The stability of macromolecules in solution results from an equilibrium between forces which tend to disperse them in the solvent and those which go to their agglutination. If the former prevail, one has to deal with a microdispersed system: a sol. In opposite cases, there is aggregation of macromolecules and flocculation. However, their agglutination can also lead to a very structured system solute + solvent: a gel. Principles governing gelation have been indexed by Rees and co-workers as early as 1969 in England. Since, two other "schools" have appeared: the one lead by Smidsrød in Norway and the other by Rinaudo in France.

At high temperature, carrageenans occur in coil. Around 30-50°C, there is a critical transition point (depending on polymer content, ion content, and ion nature) below which an ordered structure exists at the molecule level but without aggregate formation [helices, eventually associated in small soluble groups of about ten chains, called domains by Morris et al. (1980)]. Above this critical point, according to the ionic nature, a continuous three-dimensional network of aggregates develops, stabilized by specific incorporation between helices of cations whose geometry allows (Morris et al. 1980) and gelation occurs.

The ionic nature of a carrageenan salt exercises an influence on the gel texture. A potassic κ-carrageenan gel is firmer than a sodic one. Calcium salts give an elastic gel. Moreover, a ι-carrageenan gel is elastic compared to that of a κ-carrageenan because the occurrence of more numerous sulphuryl groups on molecules of the former prevents, by steric congestion, an aggregation as close as for the latter (Stancioff and Stanley 1969).

In the case of ι-carrageenan, Rees' school (Anderson et al. 1973; McKinnon et al. 1969; Rees et al. 1970; Arnott et al. 1974) proposed a gelation mechanism in two steps: a stereochemical reaction (two coils → one double helix) followed by an association of these ordered conformations in crystalline aggregates of higher dimensions. Supported by the Rinaudo school, Smidsrød et al. (1980) assumed that it is impossible to decide between the formation of double helix and the dimerization by the joining of two single helices.

In the case of κ-carrageenan, Rees' school maintains the concept of double helix and postulates that the transition state in ordered, but non-gelling, structure does not exist as it is too unstable. The schools of Rinaudo (Rochas and Rinaudo 1980; Rochas et al. 1980), and Smidsrød (Smidsrød et al. 1980) opt for the transitory state. The former believes in a dimerization of single helices, the latter in non-dimerization.

The probability that λ-, ξ-, μ-, and ν-carrageenans create a helix is nearly nil as they are short of anhydro-galactose. For this reason, they do not form any gel. λ- and ξ-carrageenans are used as thickening agents in industry. μ- and ν-carrageenans, appearing in κ- and ι-molecules in native state, have been described by Rees (1969b) as kink residues inducing discontinuities in double helices on account of the C1 conformation of the 6-sulphated-galactose residue. Thus they decrease the gelling force of κ- and ι-carrageenans; this is the reason why the industrial extracting process of carrageenans includes an alkaline transformation to eliminate them.

3.6. Anatomical localization of carrageenans in C. crispus. The strong birefringence of cell-wall compounds shows that constitutive polymers are at least paracrystalline and oriented in a parallel direction between microfibrils. The microfibrillar disorganization due to carrageenan extraction and the very low cellulose content of this alga (McCandless et al. 1977) suggest that microfibrils are carrageenan double helices (Gordon-Mills and McCandless 1977).

The intercellular matrix is not actually amorphous and contains a high proportion of this polyosides shown by its birefringence and occurrence of scattered microfibrils observable in electronic microscopy (Gordon and McCandless 1973; Gordon-Mills and McCandless 1975; 1977; Gordon-Mills et al. 1978). As sulphated content increases from the inner to the outer part of cell wall, Gordon and McCandless (1973) and Gordon-Mills and McCandless (1975) proposed that for gametophytes, the intercellular matrix has a higher content in μ-carrageenan than the sensu stricto cell wall.

The same authors (1975; 1981) also showed that the cell-wall organization of reproductive cells differs from that of other tissues in the

thallus: tetraspores and carpospores produce respectively carrageenans characteristic of the plants they give rise to.

3.7. Quaternary structure of carrageenans. Through biological control (enzymes) of the position placing of cell-wall polysaccharides, one can imagine that the formation of in vivo ordered structures sets non-covalent associations in action between these polymers and other cell-wall macromolecules (Kloareg 1984).

This type of association is largely used in the food industry. For example, the dairy industry uses the amphoteric character of milk caseins in the presence of calcium to elaborate mixed carrageenan-protein gels. Langmaack and Thiele (1958) interpreted this reaction as the formation of a polyanion-polycation macromolecular salt fixing both compounds in an ordered and oriented conformation (birefringence). The synergy between κ-carrageenan and galactomannans, as Carob gum (Ceratonia siliqua), is also frequently used. This phenomenon involves conformational transitions by mutual induction (Dea et al. 1972; Rees 1972; 1975), or "polysaccharidic allostery" (Rees 1972).

B. ECO-PHYSIOLOGICAL ROLE OF THE MATRICIAL POLYOSES

The abundance of matricial compounds in algal cell walls compared with microfibrillar ones, their polyanionic character, and the hierarchy of their primary, secondary, tertiary, and quaternary structures, suggest that besides their unique physico-chemical properties these compounds have a biological role likely specific to aquatic environment. This would be particularly the case in the intertidal belt where the ecology of plants depends on numerous factors. The most quoted functions are mechanical, hydrous and electrochemical regulations (Rees 1962; Kloareg 1981).

The cell-wall sulphurylated polyoses of littoral seaweeds seem to play a privileged role in these regulating mechanisms. It is striking to note that marine plants other than algae also contain sulphurylated polyoses while terrestrial and freshwater plants are devoid of them with some rare exceptions: the diatom Gomphonema olivaceum (Huntsmann and Sloncker 1971), the red alga Porphyridium aerugineum (Percival and Foyle 1979), and the bacterium Clostridium welchii (Darby et al. 1970).

1. Mechanical regulation

The cell-wall content of microfibrillar polyoses in Rhodophyceae is low compared to that of matricial compounds, which play a significant structural role. This seems to be an adaptation to the marine environment because gel is a structure both rigid enough to ensure a satisfying spreading out of assimilatory surfaces and yet fluid and elastic enough to absorb shocks from seawater motion (Norton et al. 1982).

Considering the qualitative aspect, Rees and Conway (1962) showed that the proportion of anhydro-galactose (and consequently elasticity) in porphyrans from Porphyra increased from sheltered to exposed habitats. On the other hand, from a quantitative point of view, Fuller and Mathieson (1972) came to doubt this mechanical regulating role for carrageenans in C. crispus because differences in content between sheltered and exposed populations were not significant.

In other respects, matricial compounds serve as lubricants to the movement of microfibrils along each other during growth (Preston 1979).

2. Hydrous regulation

Zaneveld (1935; 1969) established a correlation between the vertical distribution of the Phaeophyceae and their cell-wall thickness. Since, the most commonly accepted idea is that hydroscopic polyoses of cell walls reduce water evaporation (Priou 1962; Bérard-Therriault and Cardinal 1973; de Lestang 1974; Quillet and de Lestang 1978). Others indicate, however, no correlation between thallus water retention, thickness of cell walls and shore location (Isaac 1933; 1935; Kristensen 1968; Schönbeck and Norton 1978; 1979a and b; 1980; Dromgoole 1980; Norton et al. 1980). Nevertheless, resistance to desiccation is closely related to bathymetric level and appears to result from a physiolocial mechanism preventing dehydration (Gessner and Schramm 1971; Schönbeck and Norton 1979a; Dromgoole 1980). This would involve not only internal metabolic adaptations, as photosynthesis variations (Bidwell and Craigie 1963; Kremer and Schmitz 1973; Kloareg 1976; Wiltens et al. 1978; Quadir et al. 1979), but also the buffer capacity of the cell wall at the cellular level in relation to variations of hydrous potential resulting from hygrometric changes. Gel elasticity is a way to regulate osmotic pressure of seawater at the plasmalemma level (Kloareg 1984).

Black (1954) and de Lestang and Quillet (1972) established a positive correlation between fucoidin content in the thallus and the vertical distribution on the shore of Phaeophyceae subjected to emersion-immersion alternation. However, Fuller and Mathieson (1972) and Chopin (1985) doubt this hydrous regulating role for carrageenans in C. crispus. The former authors, as well as Mathieson and Tveter (1975), showed that content of this polyoses in mediolittoral thalli is lower than that of infralittoral. According to Chopin (1985), the seasonal pattern in carrageenan content is not statistically different in these two forms, and sea level has no influence on the carrageenan content.

3. Electro-chemical regulation

As the cell wall of marine algae contains large amounts of negative charges, it has a cationic exchange capacity (Mehta and Baxi 1976) and has to be looked at as a concentrated polyelectrolytic solution (Ayadi et al. 1980) if one considers its physiological role with regard to salinity variations.

Ionic electro-chemical properties depend on both intrinsic properties of cell-wall polyoses and on their structural state in the cell wall. Carrageenans have a selective cationic exchange capacity for divalent cations as compared to monovalent ones to which they act as filters opposing their penetration into cells (Schachat and Morawetz 1957).

C. SEASONAL VARIATIONS OF CARRAGEENANS

Several authors had observed variations in the qualitative (κ-/λ-carrageenan ratio) and quantitative (percentage of dry weight) distribution of carrageenans from naturally occurring plants of C. crispus. The causes of variation were assigned to the following factors: habitat (Black et al. 1965; Percival and McDowell 1967; Guiseley 1968; Rigney 1971; Fuller and Mathieson 1972; MacPhee 1972), nutrients in seawater (Butler 1936; Neish and Shacklock 1971; Fuller and Mathieson 1972), age of plants (Rigney 1970; 1971; 1972), date of spore release (Rigney 1972), annual variations (Rigney 1972), and geographical distribution (Black et al. 1965; Fuller and Mathieson 1972). However, no strict correlation with these different factors had been established; and results were sometimes conflicting. For example, Stancioff and Stanley (1969), contrary to Black et al. (1965), did not find any seasonal variations of the κ-/λ-carrageenan ratio.

After the discovery of the generation biochemical alternation (McCandless et al. 1973), McCandless and Craigie (1974) reassessed the significance of seasonal factors in variations of carrageenan production. It appeared that in previous studies, the sampling technique brought a bias to results: the variability of gametophyte/sporophyte ratio is the source of alterations in κ- and λ-carrageenan content. These authors came to the conclusion that in a defined site, if one considers the sexual stage of harvested plants, seasonal variations are reduced to a minimum level (slight increase at the end of summer in female gametophytes).

Mathieson and Tveter (1975) and Craigie and Pringle (1978) have also underlined the importance of taking into account the sexual cycle of C. crispus as they assigned spatial variations of the carrageenan fractions, associated with wave exposure and depth, to the fact that tetrasporophytes are more abundant at the sublittoral level except in very exposed locations (Mathieson and Burns 1975). These authors concur with Fuller and Mathieson (1972) on the reasons for the geographic variation seen in carrageenan content. They explained it as due to variations in temperature, light intensity, and seawater nutrients. Thus (Fig. 7), along the northeastern American coasts, optimal production of carrageenans takes place during a shorter period and ends earlier in the north (July-August in Nova Scotia) than in the south (August to January in New Hampshire).

Even if it is likely that a complex interaction of numerous factors is responsible for seasonal variations of carrageenans, one of them, nutrients, seems to be of particular significance. For example, Mathieson and Tveter (1975), Neish et al. (1977), Simpson et al. (1978), and McCandless and Craigie (1979) showed an inverse correlation between seawater nutrient concentration (nitrogen and phosphorus essentially) and carrageenan content

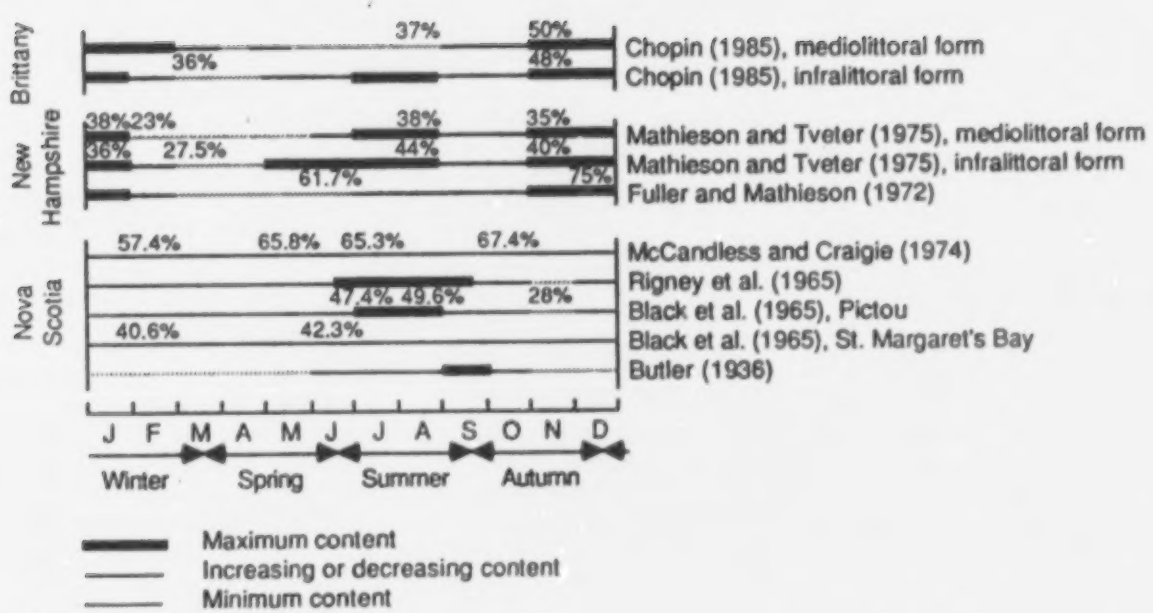

Figure 7. Distribution of carrageenan content during the year in Chondrus crispus. Percentages indicate those of dry weight.

in the thallus of C. crispus ("Neish effect"), whereas a direct correlation existed between nutrients, proteins, and growth of the alga. These results agree with those of Butler (1936) and Neish and Shacklock (1971) but disagree with those of Burns and Mathieson (1972) and Fuller and Mathieson (1972).

Chopin (1985) showed a seasonal pattern of total carrageenan content varying up to a maximum of 25% (highest content at the end of autumn/beginning of winter, and lowest at the end of winter/beginning of spring). This phenomenon is partly explained by the "Neish effect" as by other factors (see Section "I.J.", this report). Chopin (1985) also observed that distribution of carrageenans in female gametophytes of C. crispus is remarkably stable at several levels. Total carrageenan content is similar in the two forms. There is a tendency, however, for the infralittoral form to have a higher content in summer and a lower one at the end of winter and beginning of spring than the mediolittoral form. Female gametophyte carrageenans of C. crispus were identified, by IR and ^{13}C NMR spectroscopies, as κ-/ι-/μ-hybrids with a κ-dominant feature (70%). This confirms results of Bellion et al. (1983). As μ-carrageenan appears to be the only precursor, the hypotheses of Bodeau-Bellion (1983) concerning biosynthesis of these polysaccharides in this alga can be followed. Besides, κ-, ι-, and μ-structures occur all year long in the two forms. Quantitatively, there is also no seasonal variation of these three structures. The composition of the mediolittoral form (72% κ, 23% ι, and 5% μ) differs to a slight extent from that of the infralittoral form (68% κ, 24% ι, and 8% μ); but here also it is a tendency because, although more efficient than IR spectroscopy, ^{13}C NMR also has limits on the threshold on which one finds oneself, particularly when attempting to determine the proportion of μ-structure.

Therefore, it appears that at a given site, and in plants whose sexual stage is known, there is no significant qualitative and quantitative seasonal variation of carrageenan structures in extracts. Heterogeneity of phycocolloid physico-chemical properties, often recorded in the industry, seems likely to originate essentially from the following: spatial differences (mixture of C. crispus from varying locations), species differences (varying mixtures of associated species, such as Mastocarpus stellatus, which vary both spatially and temporally), and reproductive cycle-phase differences (harvest of gametophytes and tetrasporophytes together, but in different concentrations varying both spatially and temporally).

D. UTILIZATION OF CARRAGEENANS

The seaweed industry, despite a history dating back thousands of years (Naylor 1977; Michanek 1979b) in food and medicine, and a contribution in some way to almost every aspect of modern life, remains today among the most remote and least understood of the world's marine-based industries (McHugh and Lanier 1983). This is largely a product of its characteristics which are daunting in their complexity - biological, technical, and commercial. The variations in species, either in their respective ecologies and availability or in their chemical properties, define a resource and biological base of the industry which is of no small complexity. The technical and commercial complexity is exemplified by its most dynamic sector, which utilizes closely guarded technologies to extract a formidable array of seaweed colloids used

in a truly remarkable variety of commercial applications. Add to this complexity the dearth of industry data, confused, non-normalized statistics from various sources, and the not unexpected secretiveness of the few major commercial enterprises which dominate the highly competitive markets for phycocolloids, and it is not difficult to understand why little is known about this industry, outside of a relatively small number of scientists and industrialists.

1. Historical account

C. crispus has been used in food and in medicine for several centuries (Thorbjarnason 1939; Stevens 1971; Kopp and Pérez 1978). Madlener (1977) mentioned the use of this alga in food to make: blancmanges (gelating desserts), aspic jellies, and mousses in America and western Europe; thick pudding in Iceland; seaweed bread, with Laminaria saccharina, in Brittany (France); soups and stews in Boston area (USA); and stir-fried in Massachusetts (USA).

However, the real discovery of carrageenans is more recent. Recall some dates:

- 1791: Bouvier used the term "gélose."
- 1808: Turner discovered gelling qualities of hot extract from Fucus crispus.
- 1844: Schmidt carried out the first polysaccharide extraction of C. crispus.
- 1865: Blondeau analysed "goémine"; its high nitrogen content might have an appreciable nutritious value.
- 1876: Heilman noted that a 3% rate of C. crispus extract gave interesting results for starching cotton lustres.
- 1877: Heilman and Reber presented the "alguensine of Martineau" and "some gums extracted from marine algae" to the Industrial Society of Rouen (France).
- 1879: Marchand reported fraudulent use of "goémine" in manufacture of red currant jelly and made its employment prohibited.
- 1885: Miquel recommended carrageenan utilization in bacteriology.
- 1911: Daniel-Brunet Laboratory started the European carrageenan industry in France with the manufacture of the product "Coréine" for the treatment of constipation and diarrhea.
- 1914-1918: the use of carrageenans is suggested to combat the noxious effect of asphyxiating gas.
- 1921: Haas and Hill effected improvements in the extracting process of "carrageen," from that time onwards approximatively perfected.

However, one must wait until 1930-1940 to see the building of the first companies on the east coast of the United States. The industry came into its own during the Second World War due to the lack of Japanese agar. Its growth has been rapid, especially since 1960 when carrageenans started to be considered as indispensable materials in numerous branches of industry.

2. Present utilization of carrageenans

Although Thomas (1938) reported that C. crispus is smoked in Iceland, this alga is seldom directly used as its nutritious value is low (Larsen and Hawkins 1961), and it is barely digestible for human beings and domestic animals (Black 1966). It is, however, important industrially for the extracted carrageenans.

These phycocolloids present remarkable rheological properties which can be adapted with accuracy to specific utilizations by extractive or chemical techniques. As a matter of fact, taking into consideration knowledge (approximate, however, at the industrial level) of compositions in different polysaccharide structures of commonly used carrageenophytes (Eucheuma, Hypnea, Iridaea, Mastocarpus and Chondrus), one is able to forecast properties of extracts. Hence, appropriate processing and combination with these diverse seaweeds, or with other hydrocolloids, allow manufacturing of commercial products with very defined characteristics corresponding to the needs of the utilizer. Solubility in water depends essentially on content of very hydrophilic sulphuryl groups, and cations which are bound to them, as of relatively hydrophobic 3,6-anhydro-β-D-galactose. Viscosity depends on the state of polymerization [molecular weight is high and varies between 100,000 and 1,000,000 according to Black (1966) and Lecacheux et al. (1985)], concentration, temperature, and stirring. Gel force depends on the utilized structure, concentration, cations present in solution, pH, and temperature.

The stability of carrageenans in a wide pH and salinity range, their polyelectrolytic character, and their compatibility with numerous organic and mineral molecules make them advantageous as a substitute for traditional colloids from other natural sources. In fact, other colloids compete in many applications with those extracted from seaweeds. Some examples are: cellulose derivatives such as sodium carboxymethyl cellulose (CMC) and methyl cellulose; seed gums like guar, carob, sugar-cane, and locust bean gums; and plant materials like arabic and tragacanth gums, pectin, and starches.

Often the cost of colloid per unit of finished product is an important factor. Hence, the most economical result may be obtained from a combination of a seaweed colloid and one of these lower price competitors as frequently less of the former will then be required. In food preparations, however, phycocolloids have the distinct advantage of being acceptable additives in most countries. Price may not be the determining factor in a buyer's choice as quality is important, particularly in milk-based products. Availability and reproducibility are important as well. Many buyers satisfied with one particular brand or grade will stay with it despite a higher price because the risk of changing may not seem to be worth the savings. Thus, those brands already established in the marketplace often hold a very strong entrenched position.

Carrageenans are mainly used in agro-food (80% of applications), pharmaceutical, and cosmetic industries (MacLean 1954; Kloareg 1982; Boude 1983; SATIA SA,* pers. comm.).

The agro-food industry has recourse to carrageenans as additives (E 407 in European nomenclature) having the following roles:

- thickening agents (to increase viscosity of solutions): potages, soups, sauces, dressings, fish pastes, syrups, mixed yoghurts, cheese-dairy products, spreading pastes, thickened and concentrated milks, dessert creams, pie fillings, pastry creams, custards, infant foods, diet products (bulk at low calorie value);

- binding agents (to modify the texture of solids and liquids): delicatessen, mellowed flavours, fruits, bakery-product glazes, pet foods;

- gelling agents (to induce the formation of gels or to increase their rigidity): meat and fish preserved foods, aspic-jellies, pet foods, acid dairy products, flavoured gelled milks, baked custards, water-jellies, puddings, gelatinous toppings, jams, frostings, decorative creams, icings, reconstitued and imitation fruits, whipped desserts;

- stabilizing agents (to disperse suspensions and emulsions): sauces, dressings, coffee whiteners, dairy drinks (chocolate milks, flavoured milks, milkshakes), fruit drinks, aerated mousses and desserts, icing and whipping creams, ice creams (with milk, eggs, water, and sherberts), meringues, fruit pies, marshmallows;

- clarifying agents (to precipitate impurities in liquids): clarifyings of beer, ale, and wine;

- protecting agents (to preserve foodstuffs from oxidation and dehydration; associated with lecithin and ascorbic acid): frozen foods.

The pharmaceutical industry uses carrageenans in the composition of various products (Chevolot 1982; Kloareg 1982): syrups, lotions, ointments, laxatives (treatment of constipation, colitis, and diarrhea), treatment of ano-rectal diseases, binding and disintegrating agents of tablets and capsules. But they are particularly used for ulcer therapeutics: by acting as an anti-acid and protecting stomachal and intestinal walls, they isolate the latter from gastric juice and thus avoid in this manner the proteolytic action of pepsin (Black 1966). Carrageenans are also known for retarding blood coagulation (Elsner et al. 1937). They are likewise used in diet products, in making dental impressions, and as suspending agents for barium "meals" employed as X-ray contrast material.

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*SATIA SA, 50500 Carentan, France

The cosmetic industry uses them as thickening (beauty products, toothpastes), gelling (deodorant gels, solid air freshners), and stabilizing (emulsions, hair sprays, shaving creams, shampoos) agents.

Other very diversified industries also use these phycocolloids as binding (ceramics, tawing), coating (goblets, ceramic glazes), stabilizing (latex creaming, inks, insecticides, leather tanning, pigments, paintings and whitewashes, photography), and filming agents for surface processing (textile printing, upholstery, silk manufacturing, painting, and coating of paper).

3. Economic aspect

The seaweed industry is often described as a "family enterprise." If that is not true at the level of phycocolloid extraction processing, one has to admit that the harvesting and drying methods remain labour intensive. However, this situation is difficult to avoid as these techniques depend essentially on the physical and environmental conditions.

Legislation of the harvest of red seaweeds varies according to countries. In Canada, the Atlantic Coast Marine Plant Regulations control the fishing by dragraking of Irish moss (C. crispus and Mastocarpus stellatus) from the waters off New Brunswick, Nova Scotia, and Prince Edward Island, divided in districts. These regulations do not apply to the manual harvesting of seaweeds, that have become detached, along the beaches. Each district has a closed season during which harvesting is prohibited, except under authority of a special permit granted by the Minister of the Department of Fisheries and Oceans. Each harvester must be licensed by the latter, and he must harvest in only the district for which the license is issued. Not more than one license can be issued to a person in any year.

In France, harvest is allowed only during an annual period beginning 2 d before the greatest flood tide preceding June 1 and ending 2 d after the greatest flood tide following September 30. Harvest of "shore seaweeds" is reserved for residents of waterside communities. Furthermore, from a date fixed each year (end of June, generally), it is free for all collectors. Harvest of "sea seaweeds" (inaccessible on foot at equinoctial low tides) and of those growing on islands is reserved for people enrolled for naval conscription and notwithstanding pleasure sailors.

Limiting factors of this economic activity vary according to countries but can be summarized in the following manner: obsolete aspects of legislation; traditional and little mechanized harvesting methods and post-harvest treatments; obsolete and secret aspects of trade market; purchase price of raw material by processing industries increasing slower than average annual inflation rate; price of manpower; competition with other fisheries; overexploitation; variation of exploitable biomass; lack of academic knowledge and research; possible diseases, predations and pollutions; and climatic hazards.

For several decades, the main raw materials were C. crispus and M. stellatus, essentially from the Maritime Provinces of Canada (for the most part from Prince Edward Island and in less quantity from Nova Scotia and New Brunswick), New England, and France. For about 12 yr, the Philippines have

been in strong competition with the successful development of labour-intensive Eucheuma aquaculture. This country now provides nearly half of the western world's supply of carrageenophytes. The quantity of extract from Eucheuma is lower than that of C. crispus; however it has the advantage of being easily cultivated for a low labour cost. E. cottonii contains mainly κ-carrageenan, while E. spinosum contains mainly ι-carrageenan. Hence, these seaweeds present another advantage to the processor who wants to make products with the characteristics of one or the other of these structures. At the present time, culture of E. cottonii is well developed, but E. spinosum behaves erratically when cultivated and is proving more difficult to grow in reproducible quantities.

A shortage of C. crispus in the early 1970's forced the price of raw material up. This led the largest United States manufacturer to turn to Chile for Iridaea laminarioides and Gigartina chamissoi as sources of carrageenans. There was a large Canadian crop of C. crispus in 1974 as well as an expanding Eucheuma output from the Philippines; excess supplies developed and prices fell. Since then, the increasing output from the Philippines together with continuing production in Chile have ensured a sufficient supply of seaweeds to processors, but also caused a decrease in seaweed output from traditional suppliers.

The commercial world seaweed supply/production picture is in sharp contrast to that of phycocolloids. This manufacturing industry is based in only a few nations in the developed world: the United States, France, Denmark, Spain, Japan, Portugal, and the United Kingdom. Major producers of carrageenans are located in only the first three countries. Three companies are the main suppliers of carrageenans and guard their production technology secret: FMC Corp. of the United States, SATIA SA of France, and Copenhagen Pectin Factory Ltd. of Denmark (known in Canada under the name Genu Products Ltd.). The Republic of Korea was at a time the only developing country producing significant quantities of carrageenans; but its industry has severely fallen, probably because of the impact of Eucheuma farming in the Philippines. Now, entrepreneurs in certain developing nations such as the Philippines and Chile are building extraction facilities in their own country, which provide competition for the raw material.

Within the past few years a new, and less expensive, type of carrageenan has been manufactured in the Philippines (Shemberg Marketing Corp.) and New Zealand (Coast Biologicals Ltd., utilizing Eucheuma introduced to Fiji waters in 1984). Being a semi-refined carrageenan, it is sold for about 50% of the price of the refined material. Included impurities prevent it from forming a clear gel. However, there are many applications where this product is acceptable, such as pet foods. Because of the lower cost, new applications are being found. Some of this material is shipped to the major producers for further refinement. This may be cost effective as it is less expensive to ship semi-refined extract than raw material (lighter weight, no quality alteration).

The marketing distribution system for the raw material appears to be poorly organized, particularly in developing countries. The initial buying

can be done by various traders. Small traders act as middlemen to the large traders. Because of product quality variability, large traders must allow for material "shrinkage," as well as for the costs associated with any further treatment of the seaweeds. Buyers (exporters, or often, personnel of a major extractor) frequently establish strict product specifications on which sales are dependent. Exporters' purchase requirements and prices are of course heavily influenced by the buying policies of foreign users. Thus, during periods of reduced supplies and rising prices, wild seaweed collection and farming are stimulated and quality requirements are lowered. This can lead to over-production and an eventual price slump. At this time, buyers withdraw from the market once their annual targets are filled. Growers/ collectors then resort to other fisheries or sources of income. This lack of stability induces farmers to take less care with subsequent crops, producing inferior seaweeds, which results in a longer term decline in raw material. Companies either offer better prices or move into raw material production, as FMC Corp. has done in the Philippines.

Major manufacturers appear on the surface to be the main benefactors of the present marketing system. However the benefits are short term only as seaweed quality varies markedly. The formation of harvesters' cooperatives and efficient marketing structures to standardize the post-harvest treatment of seaweeds (cleaning, sorting, washing, and drying), to control the production and to stabilize prices and buying contracts, seems to be one solution to this problem (DPA Consulting Ltd. 1979; Poblete et al. 1986). This would probably not be possible without some form of government intervention. The traders sometimes provide financial and other assistance to the fishermen by furnishing, for example, subsistence loans until the crop is produced. Traders may also provide buying/delivery services for materials which harvesters require. The latter, however, do not operate on a contract basis.

The disparity between developing and developed nations in seaweed supplies versus seaweed colloid production indicates that there is a flow of dried algae of significant volume from developing to developed countries. The United States are the first world users, but Europe is the main exchange area. Nevertheless, the emerging trend seems for producers of phycocolloids in industrialized countries to establish new processing facilities in developing nations, near the source of seaweed supplies. The rising domestic costs of manufacture and pollution control, as well as the substantial savings in transport costs, may lie behind this trend. These forces, and the accelerating pace of advances in seaweed culture techniques, point toward a shift in the geographic structure of phycocolloid manufacturing, paralleling the shift that is underway in seaweed production. This shift will benefit developing countries with aquaculture capacity or potential, and is already evident in developments in Chile and the Philippines.

Any future investment in seaweed production must be approached carefully, in conjunction with an informed appraisal as to market prospects and the impacts of increased supplies, because of the present relative

balance of supply and demand in the world market. There may be room for other suppliers (if not more sales volume) simply because carrageenan processors may wish to be less dependent on one country (e.g. the Philippines) to prevent shortage due to economic or politic instability. For example, Copenhagen Pectin Factory Ltd. is developing at the present time Eucheuma farming in Indonesia. Processors would probably prefer to spread their purchases among a number of producing nations, moreso because they may supply a more consistent product (in terms of quality, quantity, and price). Because of the secrecy enforced in the production technology and the marketing expertise required by the few established producers, they would need strong incentives to enter into a joint venture with developing manufacturers.

Companies are diversifying more and more their supplies in reference also to seaweed species. To treat a single resource as an essential element is not considered cost effective. However, even if there is a significant decrease of the importance of the traditional countries supplying raw material for carrageenans (e.g. Canada and France essentially), it appears that the position of C. crispus will remain privileged (D.J. Stancioff,[5] pers. comm.; J.P. Braud,[6] pers. comm.). Companies are dependent on carrageenans from C. crispus for some applications (for example, product lines such as viscavose) because they have such exceptional physico-chemical properties that they cannot be substituted.

As the market of agro-food, pharmaceutical, and cosmetic industries is a strong market, the red seaweed industry should be able to develop in the next few decades. This will depend heavily on new and more profitable applications. One has to ascertain that industry remains, as it has always been, dependent on science because every commercial enterprise is preceded by a scientific discovery following extensive research. To resolve problems such as increasing demand for raw material (and consequently a price increase on the world market), potential risk of overexploitation and pollution, increasing cost of labour and protectionism from some producers promoting creation of new national industries, two opportunities appear: more precise determination of nature, quantity, localization, and exploitation efficiency of present or new resources, or aquaculture development. It seems that, during the last few years, the major manufacturers have found few opportunities to acquire raw materials from non-traditional sources. Rather, they have tended to improve existing acquisition methods and encourage resource management of known stocks.

Aquaculture appeared to certain authors as the most promising answer either for supplying security or standardization and control of the raw material and prices even if, in the initial period, costs of research was high and technological problems numerous to resolve (Edelstein et al. 1976; Hughenin 1976; Lapointe et al. 1976; Neish 1976; Waaland 1976; 1978; Neish et

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[5]D.J. Stancioff, FMC Corp., Marine Colloids Div., Rockland, Maine 04841, USA

[6]J.P. Braud, SATIA SA, 50500 Carentan, France

al. 1977; DeBoer 1978; Lapointe and Ryther 1978; 1979; Michanek 1978; Ryther et al. 1978; Fralick et al. 1981; Lapointe 1981; Shacklock and Doyle 1983; van der Meer 1983).

Attempts to develop C. crispus cultivation techniques have been ongoing in Canada and France since the early 1970's (for review: Braud and Delépine 1981; Bidwell et al. 1985). The bulk of the costs in Canada have been provided by federal government agencies, whereas it was private investment in France. Tank systems were built and numerous parameters were tested: forms and sizes of tanks; agitation of water and seaweeds; inoculum density; flushing rates and timing; quality, quantity, and frequency of nutrient additions; carbon dioxide enrichment; temperature; light intensity; photoperiod; epiphytism, etc. A commercially viable cultivation system must be continuous, and easily and cheaply operated by optimal, but not necessarily maximal, integration of these different parameters. The final product must be either less expensive than that obtained from the wild harvest or substantially better in quantity and/or quality. After about 15 yr of research, it appears, however, that aquaculture cannot yet compete with the wild harvest in temperate regions (Bidwell et al. 1985). This is in part due to high operation and labour costs, and inadequate solar and thermic regimes.

With the development of aquaculture (which has already occurred for carrageenophytes other than C. crispus, especially Eucheuma in the Philippines), however, another problem arises: the privatization of seaweeds, wherein this renewable biomass, although considered a public wealth, is subject to management plans within which the goals are themselves not always consistent (maximal profits for industry, maximal social benefit, optimal bio-ecologic management, etc.).

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